WESTERN SPRUCE BUDWORM IMPACT MODEL CALIBRATIONS

by

TOM NICHOLS

Final Report to CANUSA/Spruce Budworms - West

March 10, 1984

MAR 1 3 1984

J. Colbert

United States Department of Agriculture
Forest Service
Intermountain Forest and Range Experiment Station
1221 S. Main
Moscow, ID 83843

Reply to: 1630

Date: March 26, 1984

Tom Nichols
6425 65th Avenue NE
Seattle, WA 98115

Dear Tom:

Thank you for promptly writing up your report and sending a copy to me. Your attention to these details ought to pay off, so to speak!

It looks like all the extra effort has been worthwhile to the CANUSA program. Your results make sense, and the unique approach illustrates an interesting scientific investigation. I hope you will publish this in Forest Science or the Canadian Journal of Forest Research. It is interesting and important work.

Toward that end, I am recommending to Jim that an additional contract be granted to you to prepare a manuscript which is ready to submit to a Journal. Contract competition could be signaled when the manuscript has been through CANUSA solicited review (Al Stage and Al Thompson are likely candidates) and then found acceptable by Martha Brookes and Jim or me. Then the program would pay you and agree to pay the Journal page charges. You would have to agree to answer Journal reviewers' comments on your own, but that shouldn't be hard if Stage and Thompson have reviewed the manuscript. Since I'm not a contract officer, I haven't any clue how the details should be worked out. Perhaps they already have been.

The work looks good and I think your report satisfies contracting requirements, BUT, the report needs help! Specific comments follow:

Page 1, paragraph 2: "It was noted in this earlier study, however, that nondefoliated trees..." You have stated that nondefoliated trees have... something...and, therefore, the models may underestimate the effects of the budworm. The connection between nondefoliated trees and budworm has not been spelled out in this report. Therefore the report does not stand on its own.

Clean up the language if you can (Martha could help): "It was noted in..." could read "The study found..."

MAR 30 1984

Page 1, INTRODUCTION: Rewrite the introduction so that it describes the report rather than the findings of an earlier study. A summary of the current findings could be included. You need an overview or road map to the study and presentation. On page 4, you start with non-host correlation, but, as a reader, I wondered why it was even an issue!

Page 6-7: What is the y-axis? How can predicted and observed be plotted in Figure 3A. Perhaps separate symbols for each would be helpful.

Again, how does this part of the study fit in?

Page 8-10: What does the hand-drawn line signify?

General comment: Perhaps you could shade the background of the figures indicating which years are outbreak years and which are not. This would serve to strengthen the visual message

Page 25: The first time I read the paragraph starting "No logical explanation..." I didn't know what sudden growth you were talking about. Perhaps you have too many figures; each one isn't quite worth 1,000 words, and I felt confused with the mass of data. This is a critical part of the analysis and the observations represented in figure 25 seem to have slanted the rest of the study. More discussion is needed.

Page 27: I got confused! The confusion relates back to page 6--you have combined Analysis, Results, and Discussion under one heading. How about a Problem Statement, Methods, Results, and Discussion. You may need several of these sequences or a list of problems, followed by parallel presentation of methods, results, and discussions. I think methods sometimes include analyses. How you measure data is one type of a method, how you transformed data and computed statistics is another method. I think you need to clearly show the steps used to compute various new variables and, at times, the steps used to compute a test statistic. You have gone far in meeting this need, but I felt the presentation lacked organization and some critical steps in your thinking.

Page 41: Review Zahner and Stage (1966) in enough detail so the reader doesn't have to read that paper to understand this one. Did they show how to compute moisture stress and show how to relate it to annual growth? The answer is yes--as I see on page 47.

Page 47: Write the model form and present the fitting as an experiment: Hypothesis, Methods, Results.

Page 48: This model is different from the one described on page 47. Why are the calculations of B_2 to B_6 done the way they are? I'm confused!

Page 59: Al suggested the following as a model which will provide a flat top end (I have no idea if it is the correct form to use):

$$RHTI = k(1-\exp(-BX))$$

Again, Tom, thank you

Sincerely,

B. Benedict

for NICHOLAS L. CROOKSTON
Research Associate

cc:
J. Colbert, CANUSA-West ✓

Tom Nichols
6425 65th Ave NE
Seattle, WA 98115

March 10, 1983

Dr. Jim Colbert
U.S.F.S.
CANUSA/Spruce Budworms-West
P.O. Box 3890
Portland, OR 97208

Dear Jim:

Enclosed is the final report for my project. You will note that it is comprehensive, covering all three items (Items 1 and II are essentially the same as the interim reports - I just wanted to include all of them together in one report). I am very happy with the results of the weather correlations. Finally, after all this time, the data started falling in place. I'm also sending a copy of the report to Nick. I'm sure he'll be contacting me with questions about it. I just spoke to him a few weeks ago, so he's expecting the good results.

Needless to say, I feel great right now, with the load of this study off of me. I've never looked at one subject for so long a time. Although I still have to rewrite the reports into a different form for my dissertation, the hard part is done.

I'm excited about this next phase of the research. I've been thinking about it for a long time, but have not been able to act on it. Incidentally, I would have no objections to additional funding if you happened to have extra funds laying around (please don't be offended by my asking - I thought it would be worth a shot!).

I've got leads on a few more job possibilities, which I'm checking into now that this work is done. I'll let you know about them later.

As always, I appreciate everything you've done for me. Hope all is well.

Regards,

Tom

Tom

March 10, 1984

Invoice for personal contract:

WESTERN SPRUCE BUDWORM IMPACT MODEL CALIBRATIONS

Order number: 40-04H1-4-5063

Item #3:

WEATHER CORRELATION CALIBRATION

Labor, supplies, materials, computer time $ 3110.00

Submitted by:

Tom Nichols
6425 65th Ave NE
Seattle,WA 98115

(206)-543-5772 days
(206)-524-3310 nights

Submitted to:

CANUSA/Spruce Budworms-West
PNW Forest and Range Experiment Station
P.O. Box 3890
Portland, OR 97208

Billing Address:

U.S.D.A.
National Finance Center
P.O. Box 60075
New Orleans, Louisiana 70160

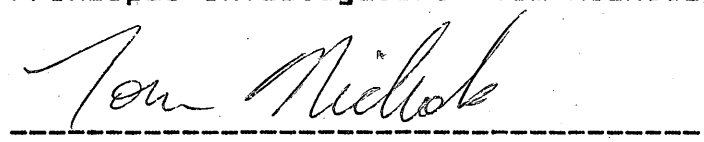
Final Report for Personal Contract:

WESTERN SPRUCE BUDWORM IMPACT MODEL CALIBRATIONS

Including Items:

1. DEFOLIATION VARIABILITY STUDY
2. NONHOST CORRELATION CALIBRATION
3. WEATHER CORRELATION CALIBRATION

Principal Investigator: Tom Nichols



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March 10, 1984

Submitted to:

CANUSA/Spruce Budworms-West

ORDER NUMBER: 40-04H1-5063

Western Spruce Budworm Impact Model Calibrations

TABLE OF CONTENTS

INTRODUCTION 1

NONHOST CORRELATION CALIBRATION

Methods and Procedures 4

Analysis, Results and Discussion 6

WEATHER CORRELATION CALIBRATION

Methods and Prcocedures 41

Analysis, Results and Discussion 43

SUMMARY AND CONCLUSIONS 60

LITERATURE CITATIONS 62

APPENDIX

Defoliation Variability 63

INTRODUCTION

Damage to forest stands due to defoliation by the western spruce budworm (*Choristoneura occidentalis*) has occurred periodically over vast acreages in the western United States (Johnson and Denton 1975). In order to quantify this damage so that forest managers can make rational decisions regarding the budworm, the CANUSA/Spruce Budworms-West program funded a number of integrated research projects to develop models for predicting insect and tree dynamics.

One of the projects, "Growth Impacts on Host Trees due to Western Spruce Budworm Defoliation on the East Slope of the Washington Cascades" (Scott and Nichols 1983), looked specifically at the effect of defoliation on height and diameter growth of Douglas fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) trees. The project presented working models linking defoliation levels and attack duration to growth loss. It was noted in this earlier study, however, that nondefoliated trees appeared to have greater than average growth rates during the years modelled (Figure 1). As a result, the models that were presented may underestimate the effects of the budworm.

It was suggested that corrections for growing season should be made in the models, and the present study was funded to attempt to carry this out. Two methods for predicting growing season effects were studied. The first method makes use of the relationships between host and nonhost tree growth. The second method uses weather and site data to predict soil moisture

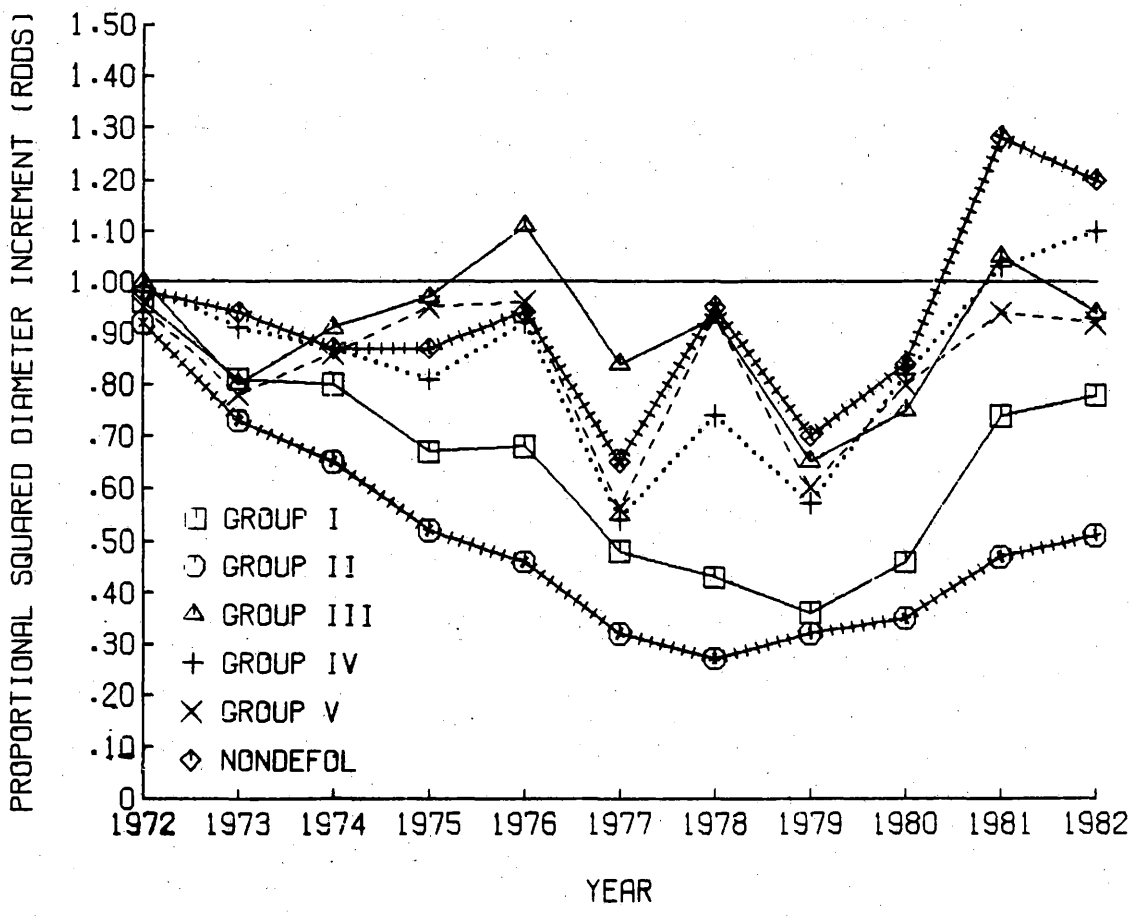

Figure 1. Relative growth of defoliated and nondefoliated trees sampled in 1982, averaged by sample area.

stress, then uses this data to predict growing season effects. Since this project is a continuation of the earlier project by Scott and Nichols (1983), most of the specific information on sampling procedures, etc., is discussed in the earlier report, and the reader is referred to that report for more detailed information.

An additional item covered in this report is a listing of defoliation levels of trees in this study and their variance, broken into different subgroups. Since this item is simply a set of tables and not directly related to the model calibrations, the tables are listed in the appendix and no further discussion of this item is contained in the report.

********* NONHOST CORRELATION CALIBRATION *********

METHODS AND PROCEDURES

Locations of the sample areas are shown in Figure 2. From each of the 5 general areas, 15 nonhost trees were selected for sampling. Most of these trees were ponderosa pine, but a few lodgepole pine and white pine were also selected. The trees were growing close to the stands where the host trees were sampled in 1982, but were far enough away so that competition with host trees was nonexistent or minimal. Trees in stands that had been manipulated (naturally or by man) during the past 30 years were avoided.

Two opposing side-hill increment cores were taken from each tree at breast height, and DBH, tree species, and location were recorded. The cores were stored in paper straws and allowed to air-dry for two months prior to mounting. After preparation and cross-dating, ring widths from each of the past 60 years were measured to 0.01 mm on a Bannister Incremental Measuring Machine. Accuracy of the cross-dating was rechecked by comparing the ring width data between trees for selected years.

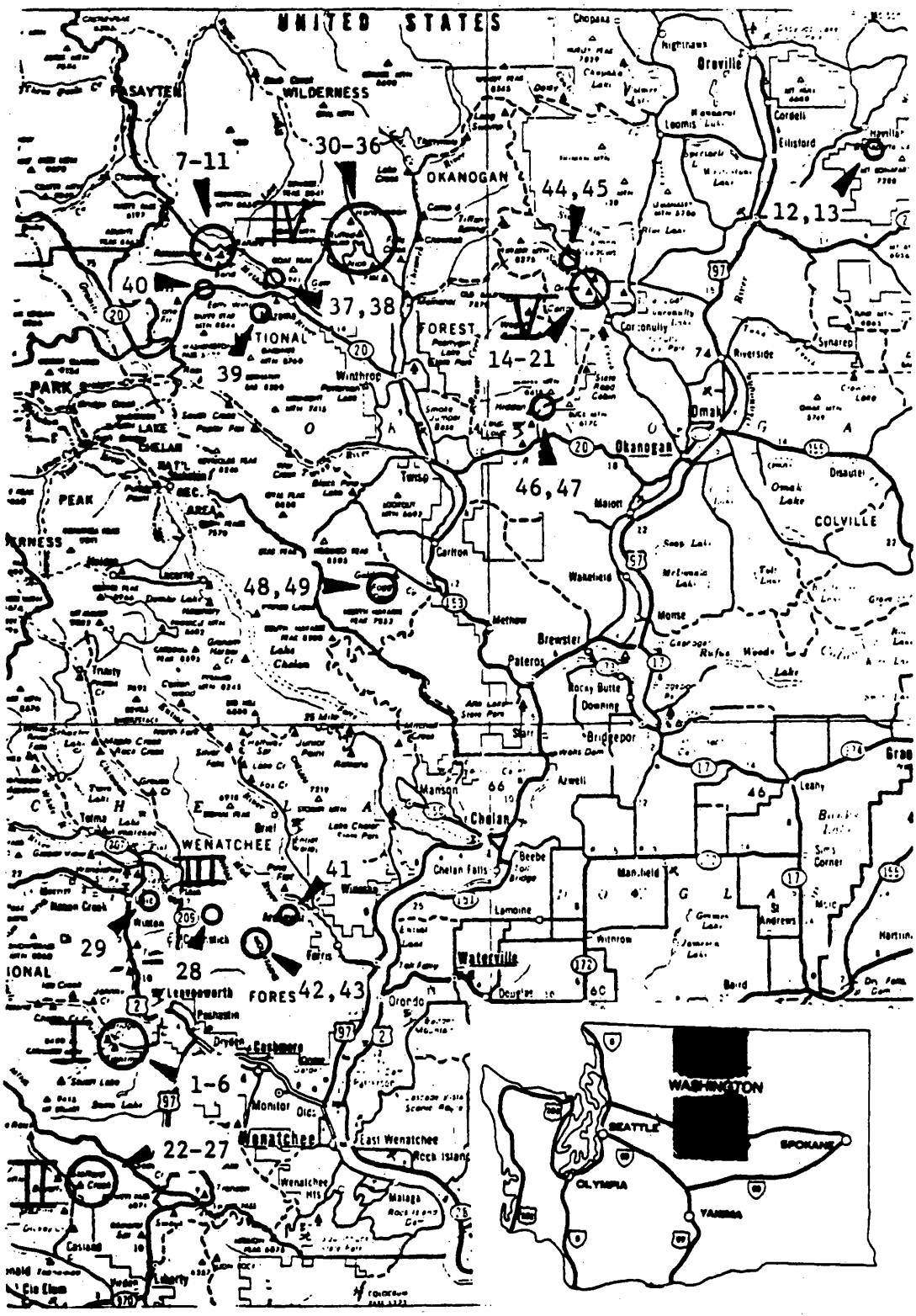

Figure 2. Locations of stands monitored throughout study. Roman numerals designate sample areas referred to in text.

ANALYSIS, RESULTS AND DISCUSSION

In the earlier study (Scott and Nichols 1983) annual growth of the host trees was predicted using calibrated predictions from the Stand Prognosis Model (Wykoff et al 1982). This method could not be used with the nonhost trees, however, since it requires stand data that was not available. An alternate method for predicting growth was attempted using cumulative tree growth as a function of time, similar to the method introduced by Mika (1983), except that he used cumulative diameter, while the present study used cumulative basal area. The model fit was :

$$\text{basal area} = B0 + B1 * \text{time} + B2 * 1/\text{time}$$

Time was equal to the number of years since 1922. After annual basal areas were predicted, increments (BAI) were calculated by subtracting basal area in the preceding year from basal area in the present year.

Various combinations of years were compared for predicting growth. One combination used the preceding twenty years to predict basal area (i.e., 1923 to 1942 basal area to predict 1943 basal area, 1924 to 1943 area to predict 1944 area, etc.). Examples of observed and predicted growth using this combination are shown in Figures 3A and 3B. Another combination tried used the preceding and following ten years to predict growth (for 1973 to 1982, the number of following years was lower). Examples using this combination are seen in Figures 4A and 4B.

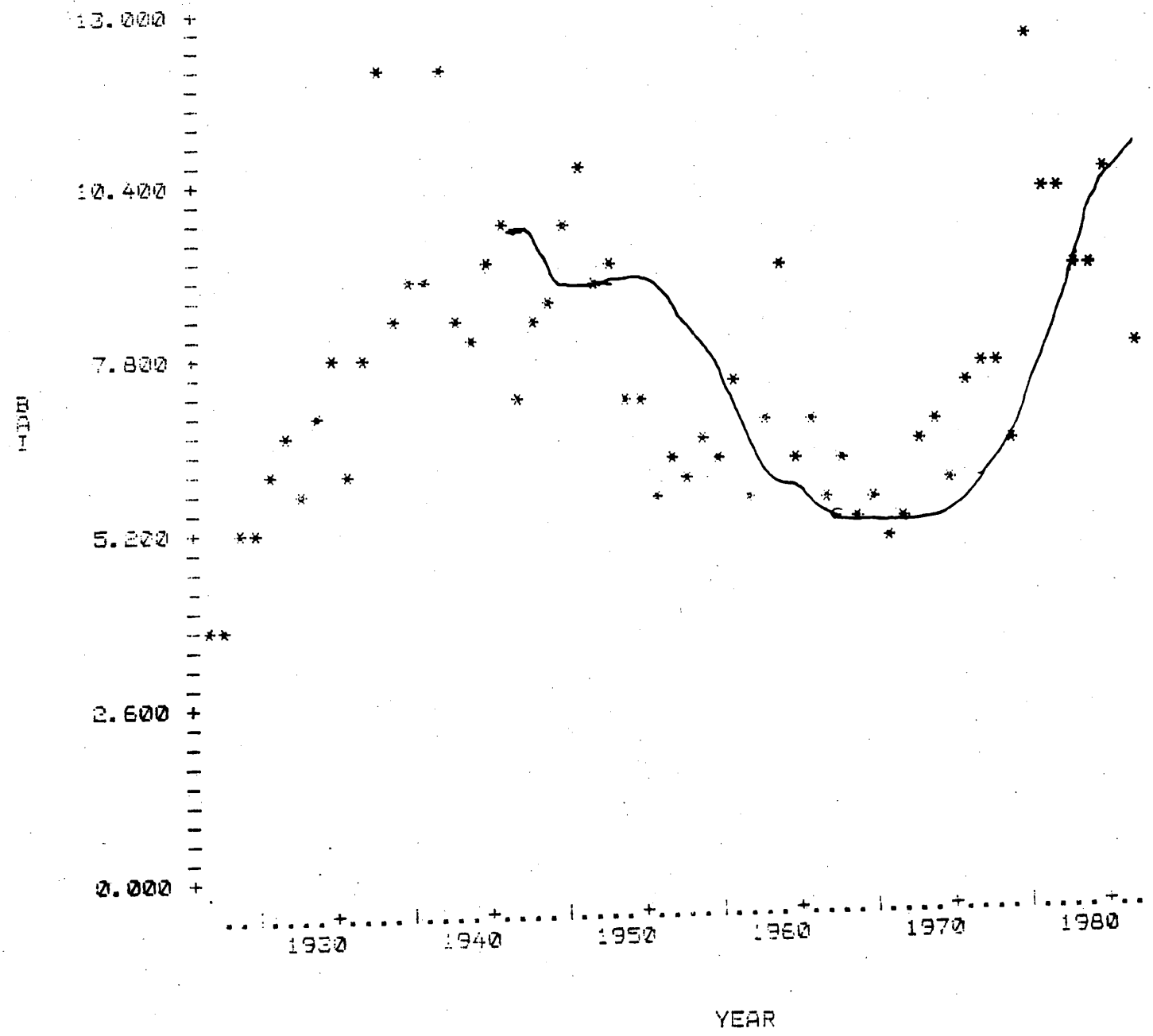

Figure 3A. Predicted and observed BAI for Tree I12 using past 20 years for prediction.

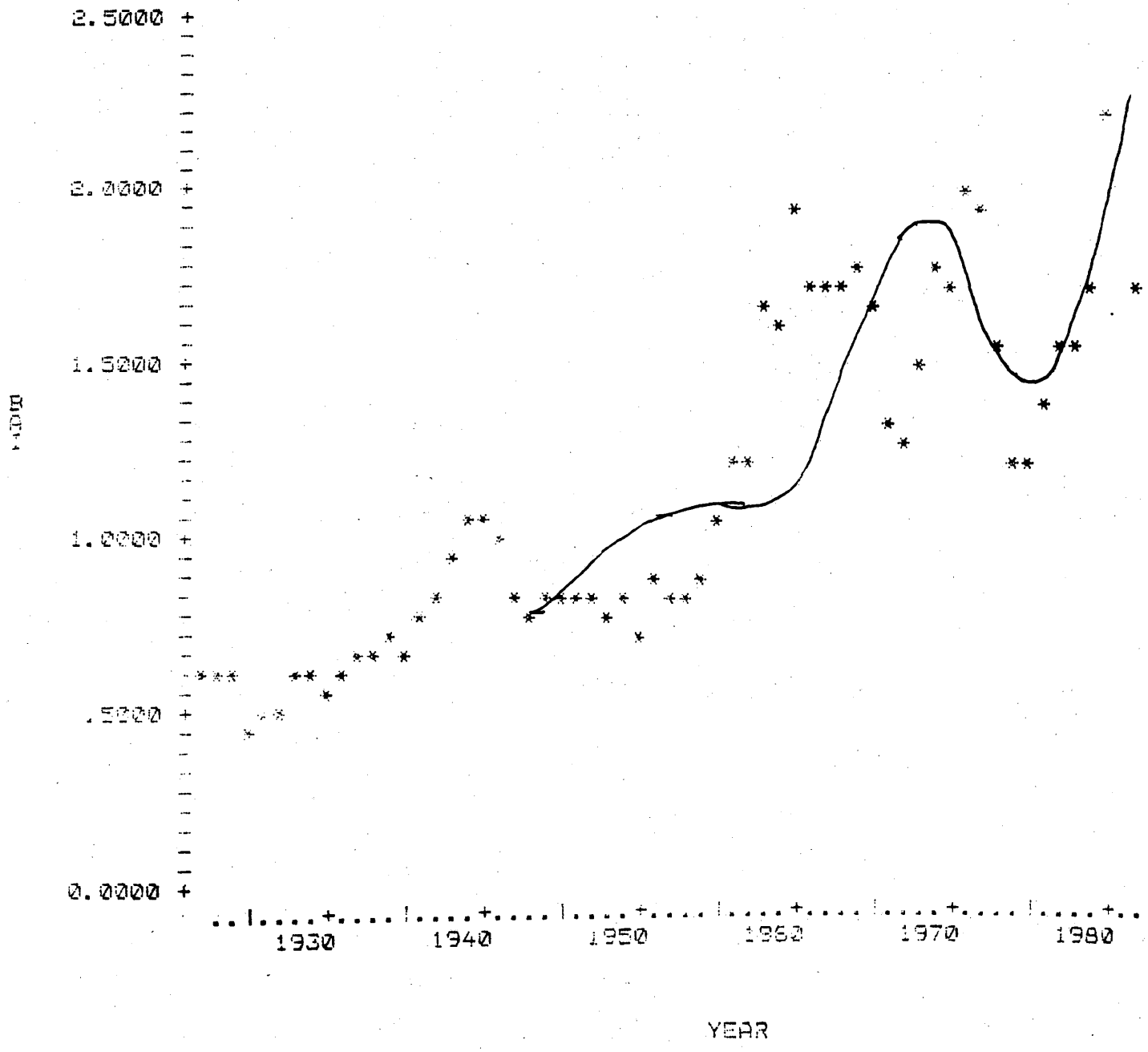

Figure 3B. Predicted and observed BAI for Tree I10 using past 20 years for prediction.

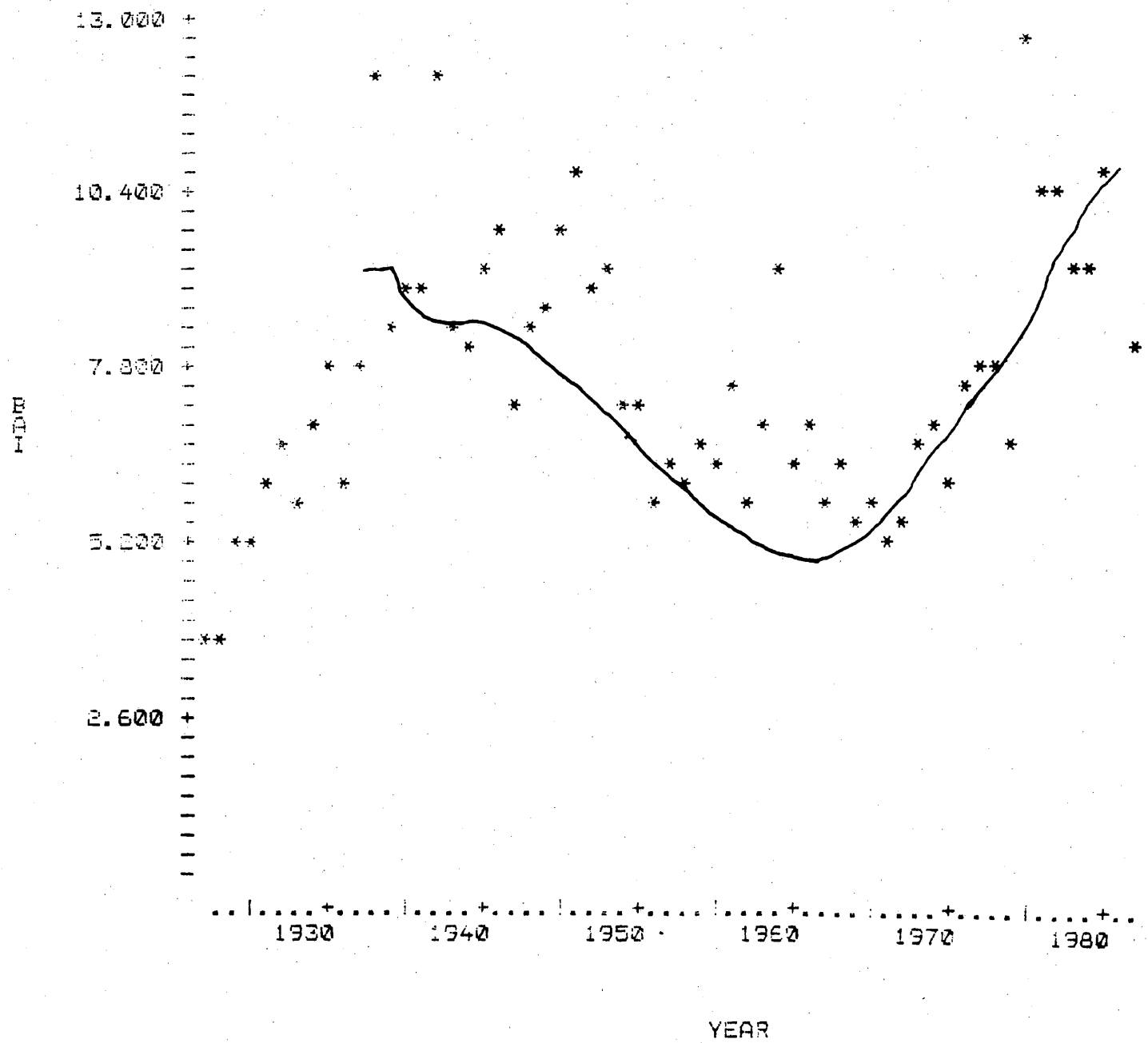

Figure 4A. Predicted and observed BAI for Tree I12 using past 10 and following 10 years for prediction.

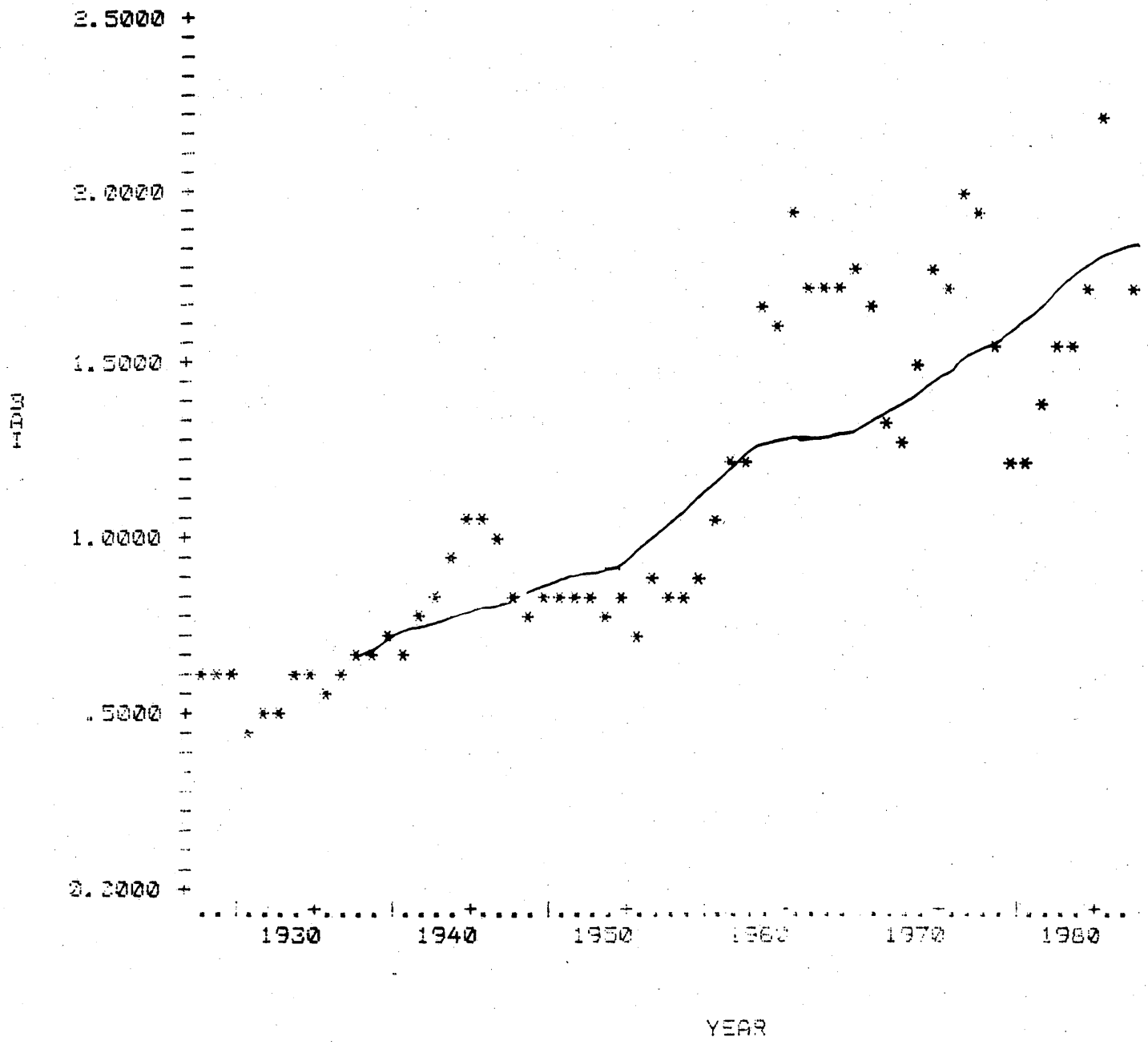

Figure 4B. Predicted and observed BAI for Tree I10 using past 10 and following 10 years for prediction.

Another combination broke the modelled years into three periods. Growth from 1923 to 1942 was predicted using this twenty-year period, growth from 1958 through 1972 was predicted using this fifteen-year period, and 1973 to 1982 growth was predicted using 1968 to 1982 growth (the logic behind these periods is made clear in a later discussion). Predictions using this combination are seen in Figures 5A and 5B. It is apparent that the combination chosen can greatly affect the individual tree/year predictions.

Using each of these combinations, relative basal area increment (RBAI), which is mathematically equivalent to relative squared diameter increment (RDDS), was calculated for each nonhost tree for each of the past sixty years (RBAI = MBAI/PBAI ; MBAI = measured BAI, PBAI = predicted BAI). These proportions were then averaged for each drainage each year. Although Figures 3 through 5 showed that annual estimates of individual tree growth varied depending upon the combination of years selected for the model, the results for the averaged proportions were fairly similar for all of the combinations used.

An example of the averaged annual proportions for each area is shown in Figure 6. As noted earlier, Figure 1 presented evidence suggesting that the 1981 and 1982 growing seasons were substantially above normal. In contrast, when the cumulative basal area models were used, in most cases predicted growth was average or below average during these years (i.e., RBAI(1.00). It appeared obvious that there was a problem with the models and/or the data.

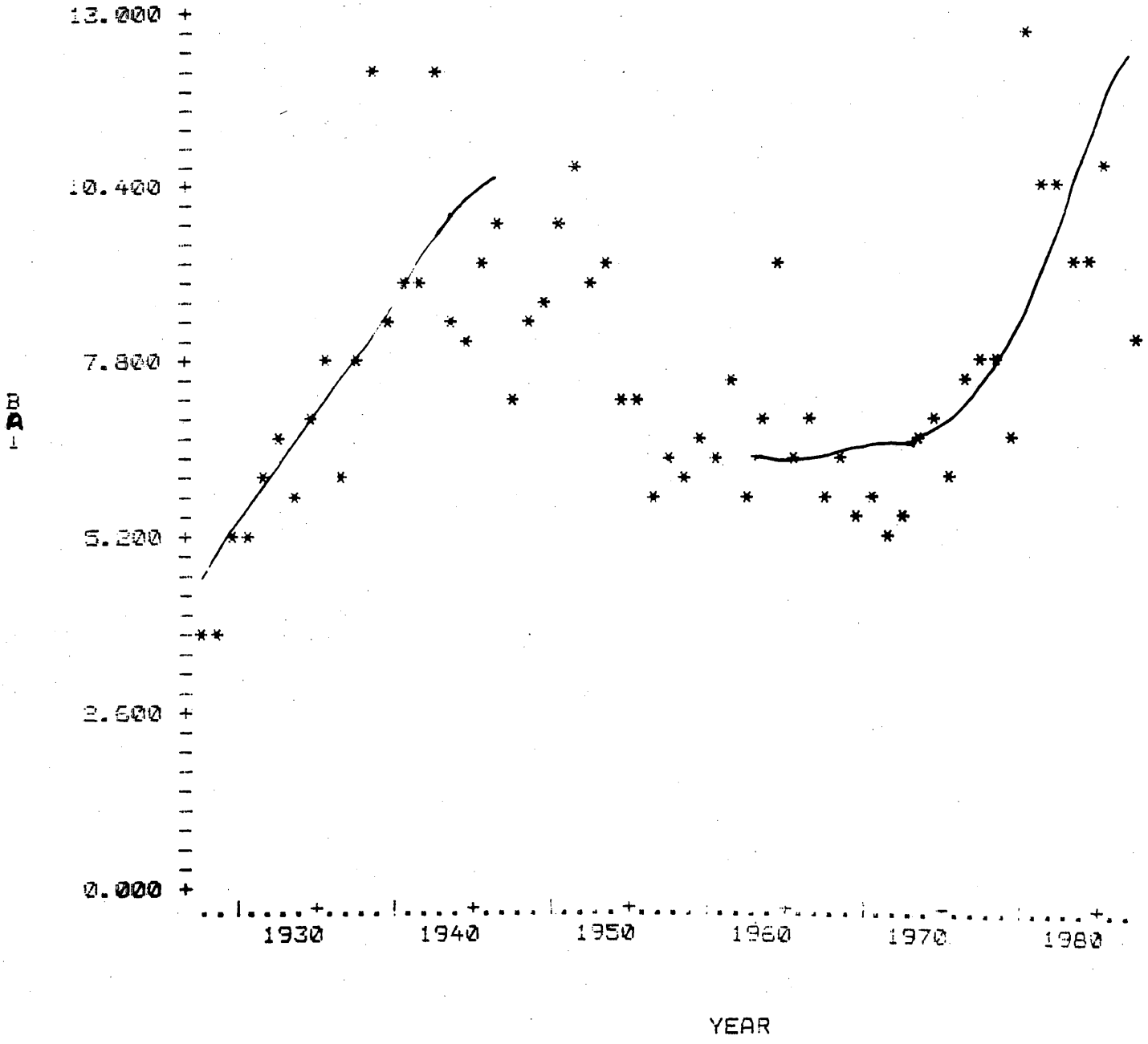

Figure 5A. Predicted and observed BAI for tree I12 using 20., 15, and 15 year periods for prediction.

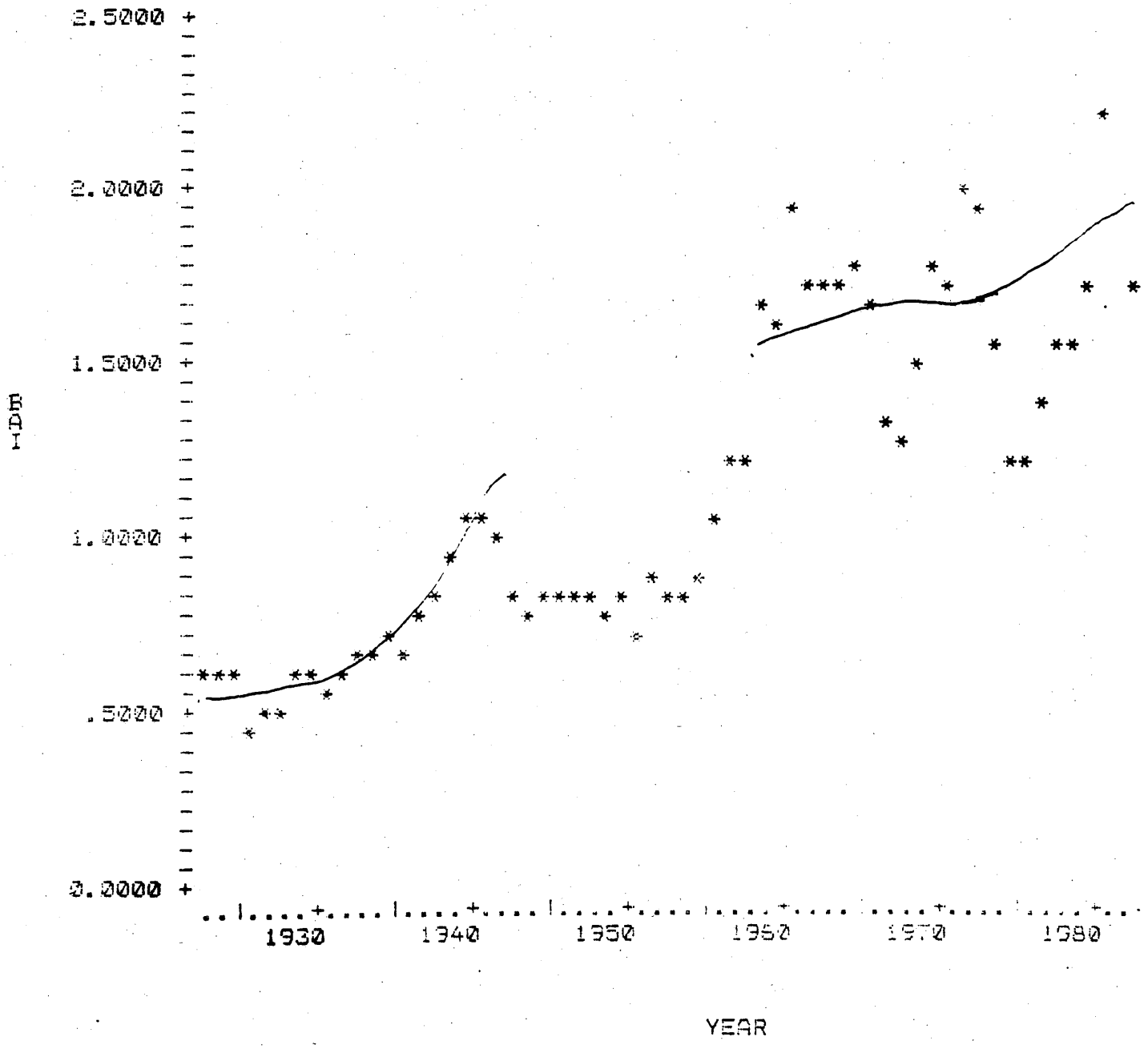

Figure 5B. Predicted and observed BAI for Tree I10 using 20, 15, and 15 year periods for prediction.

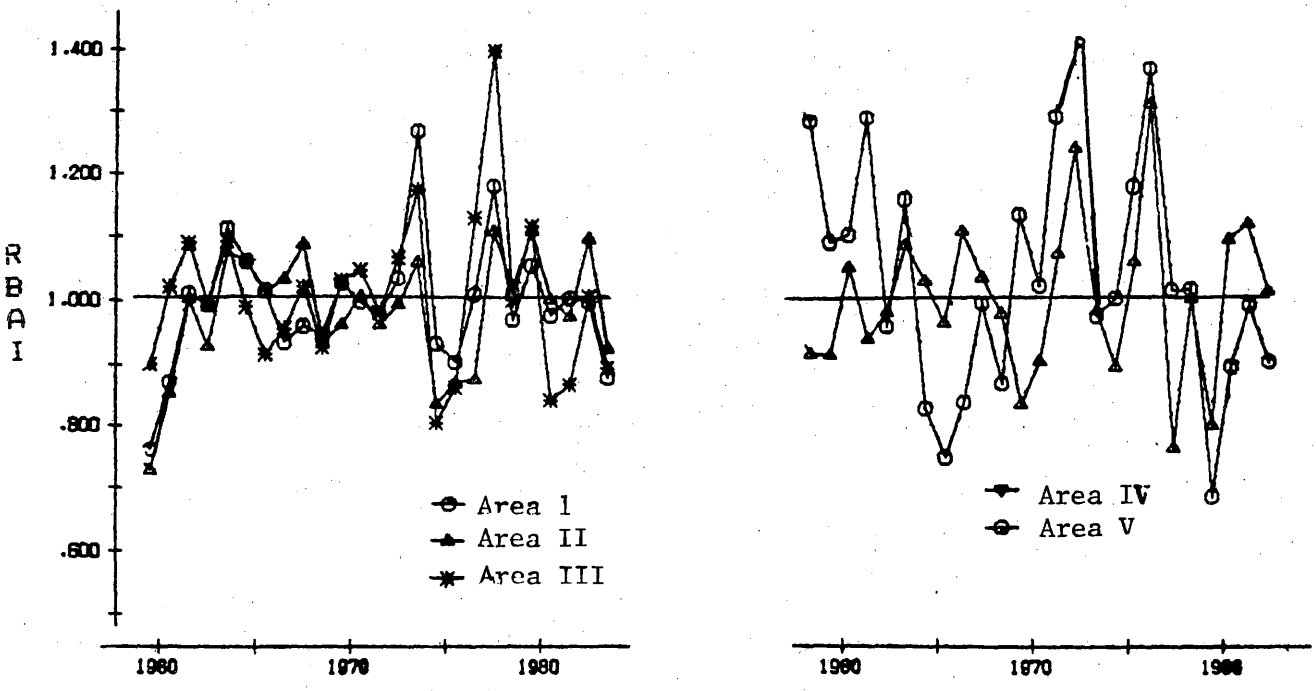

Figure 6. Average relative BAI of nonhost trees by sample area - Areas I, II, and III (left), and areas IV and V (right).

To obtain a look at the absolute growth values, the BAI's for the 15 trees in each area were averaged for each year and plotted (Figures 7A to 7E). These graphs indicate that the nonhost trees in most of these areas had a sudden substantial increase in growth in the early to mid-1970's, then growth leveled off at these higher rates. Checking the raw data for each of the trees and observing the increment cores revealed that all but one or two trees in each area had this increase in growth. In contrast, growth of several nonhost trees growing in mixed host/nonhost stands in these areas did not exhibit this major increase in growth (Figures 8 and 9).

It is doubtful that weather was a major factor in this increase in growth, since the trees growing in the mixed stands did not exhibit this growth pattern. Further substantiating this, precipitation records from these areas do not show a cause for this increase (Figures 10A and 10B), and the analysis in the second part of this study did not indicate that a major increase in growth should have occurred during these years.

The trend of an abrupt increase followed by a leveling off of growth suggests a change in tree competition favoring the nonhost trees. As noted earlier, however, none of the trees were selected from stands which showed manipulations in the recent past. Also, the trees were selected such that release of the nonhost trees by defoliation of the host trees should have been minimal or nonexistent. In addition, most of the nonhost trees were large old growth trees (25 to 40 in DBH). One would not

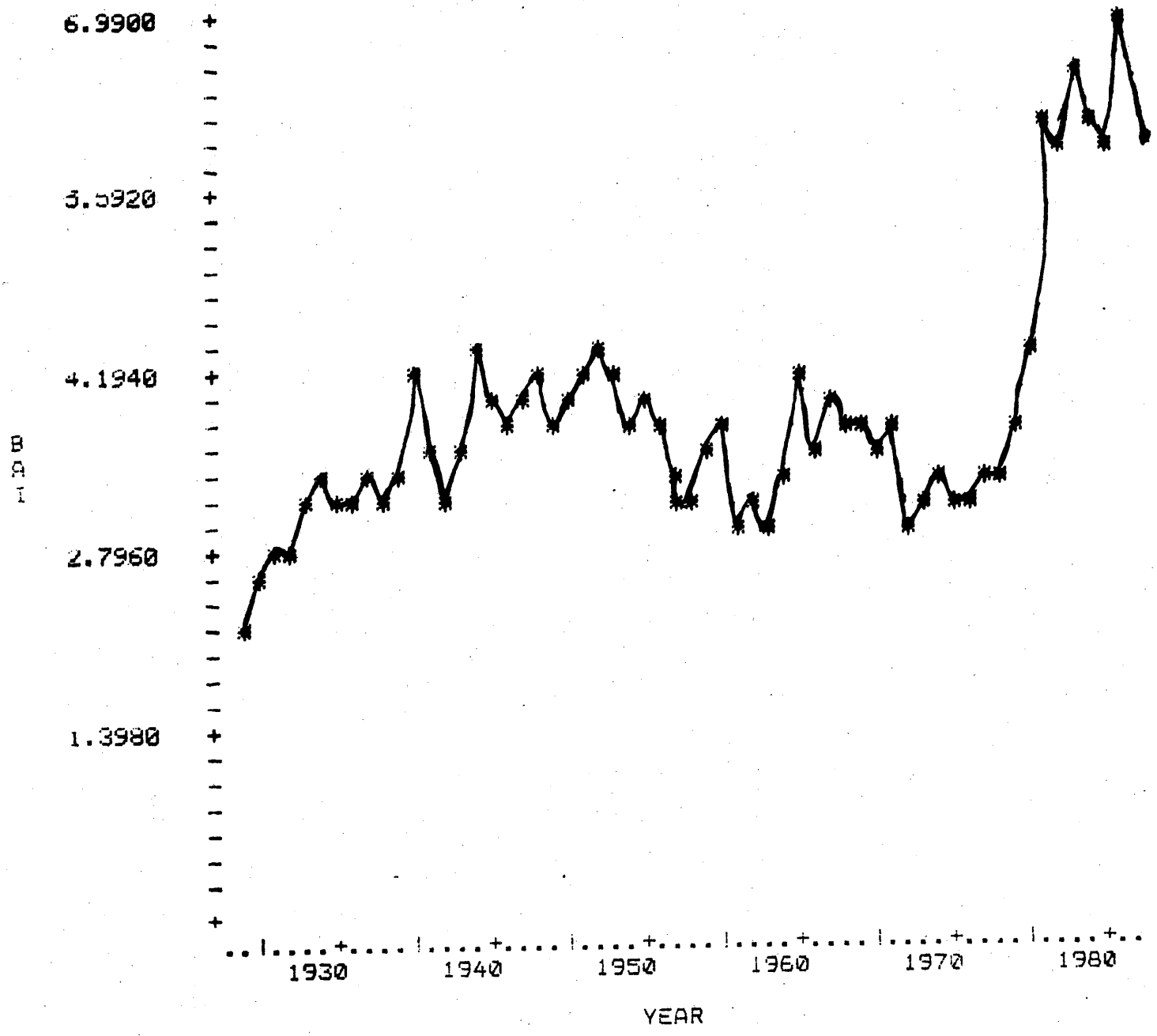

Figure 7A. Average BAI of fifteen nonhost trees from Area I by year.

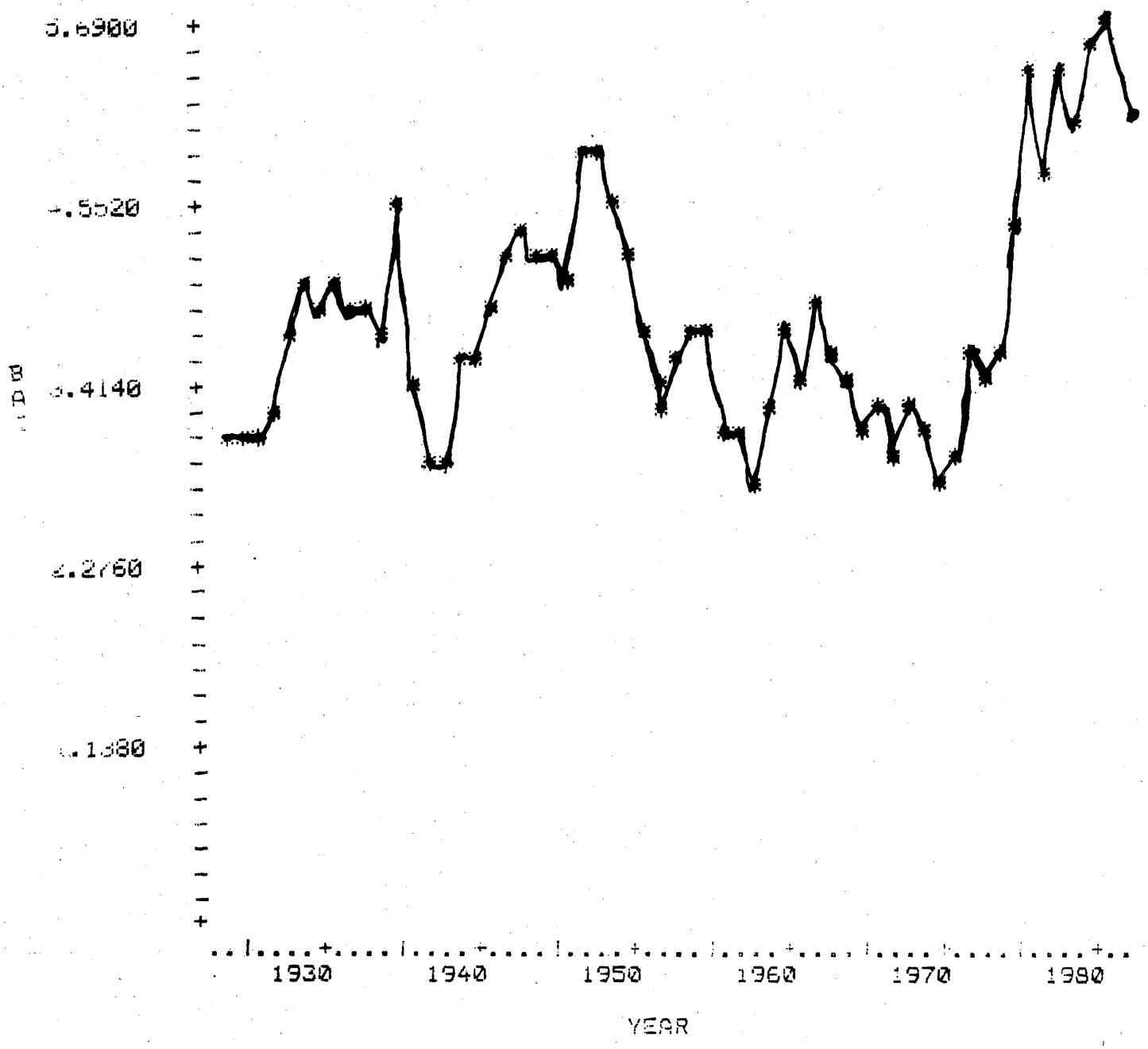

Figure 7B. Average BAI of fifteen nonhost trees from Area II by year.

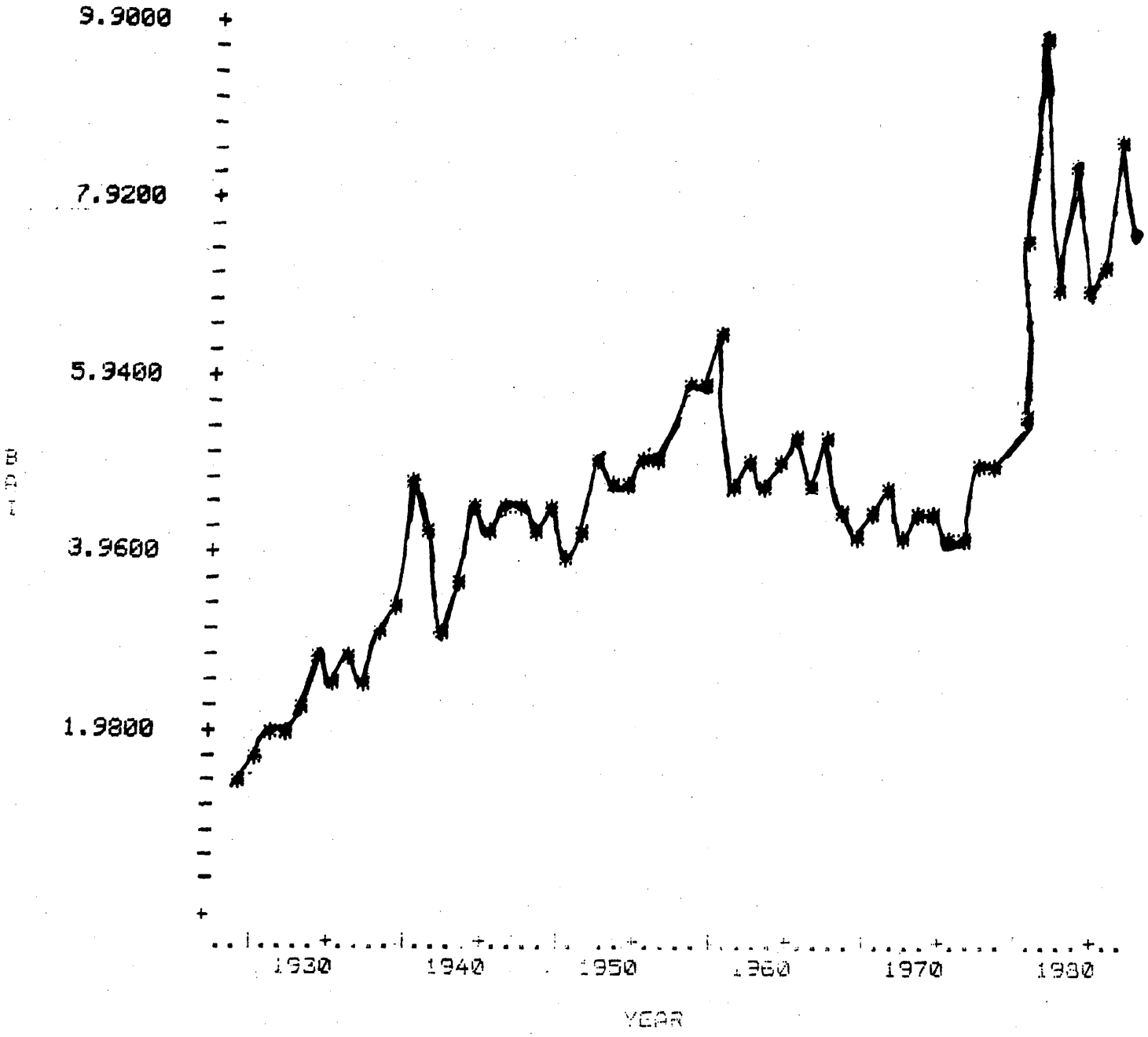

Figure 7C. Average BAI of fifteen nonhost trees from Area III by year.

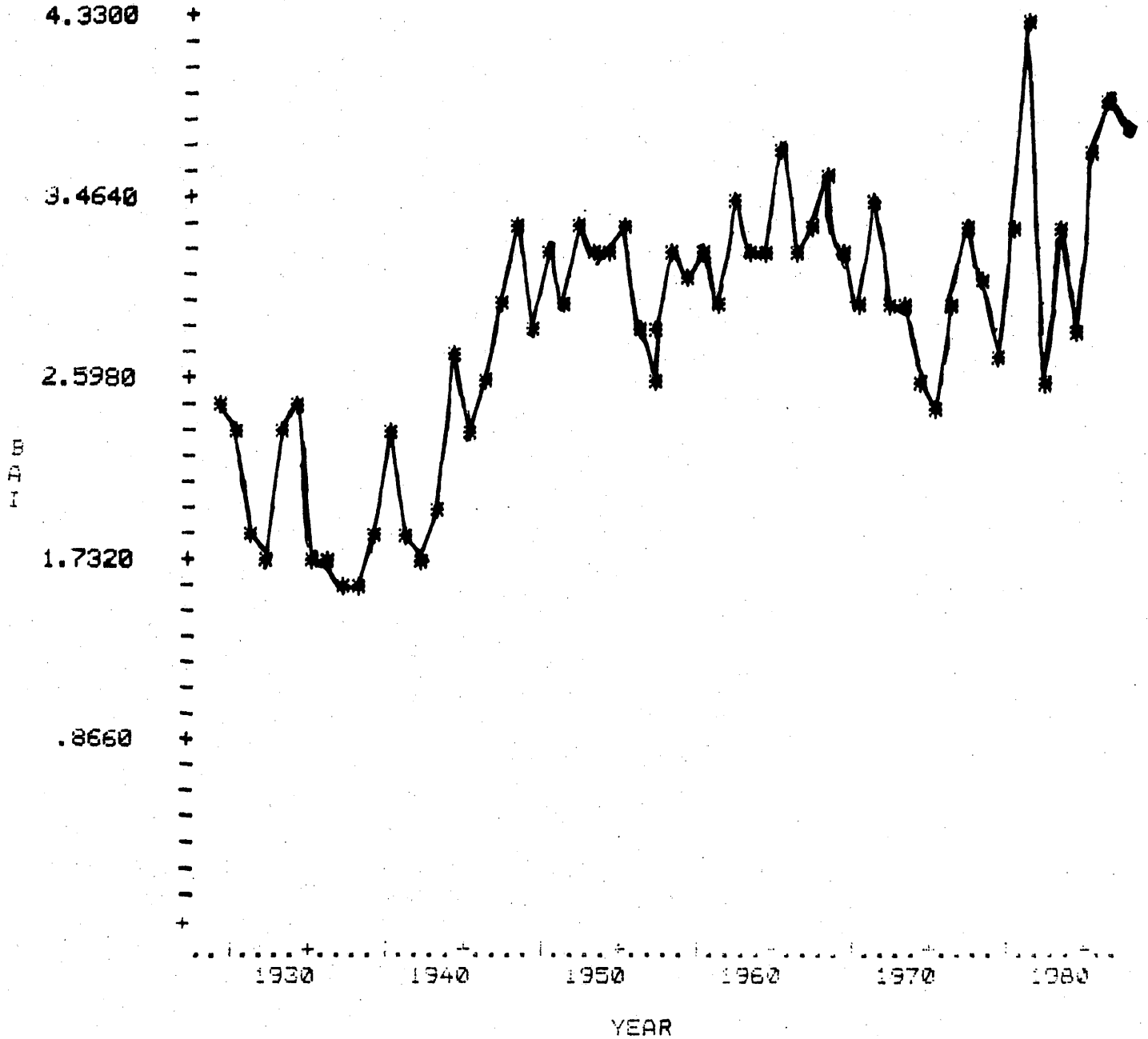

Figure 7D. Average BAI of fifteen nonhost trees from Area IV by year.

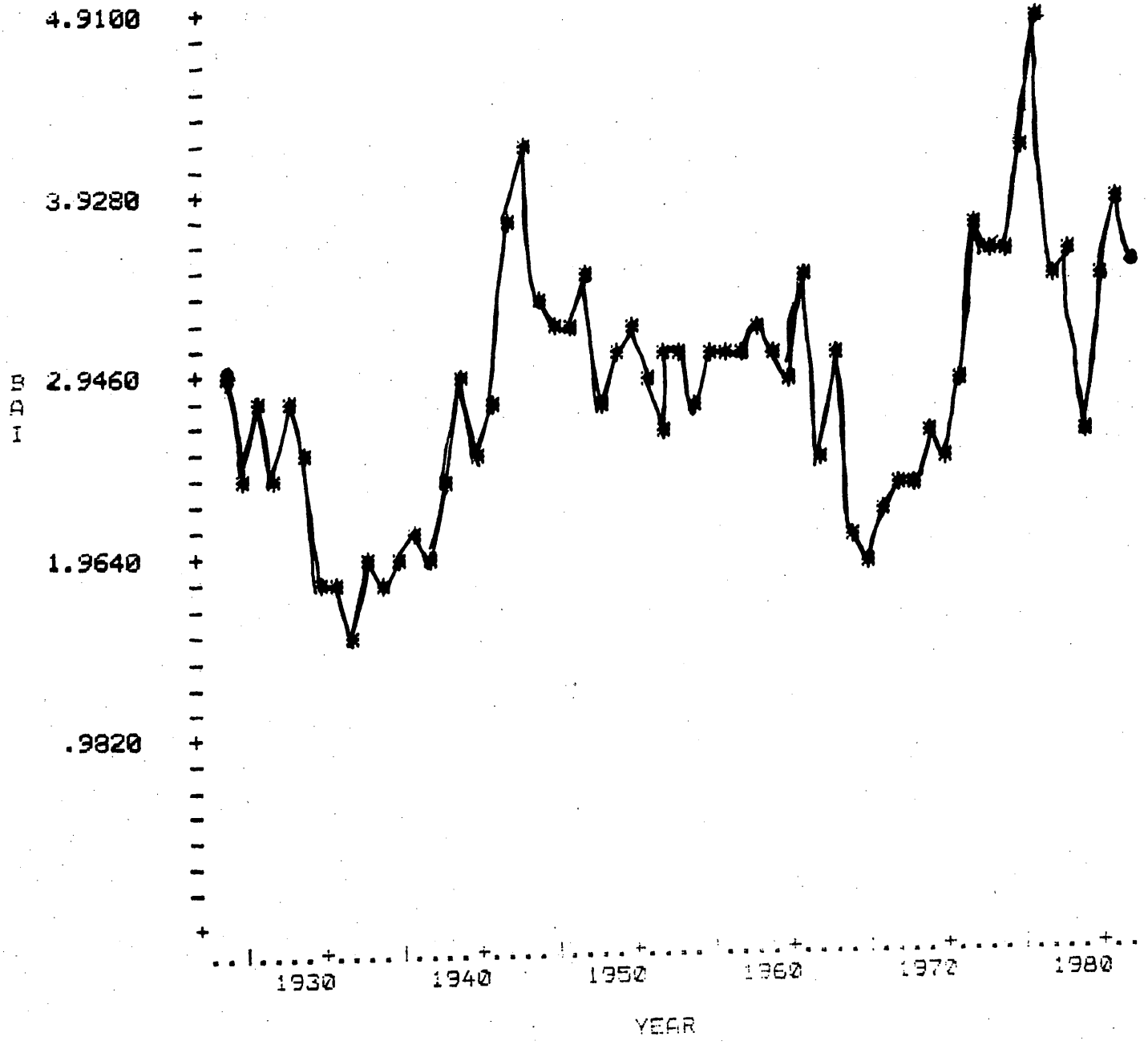

Figure 7E. Average BAI of fifteen nonhost trees from Area V by year.

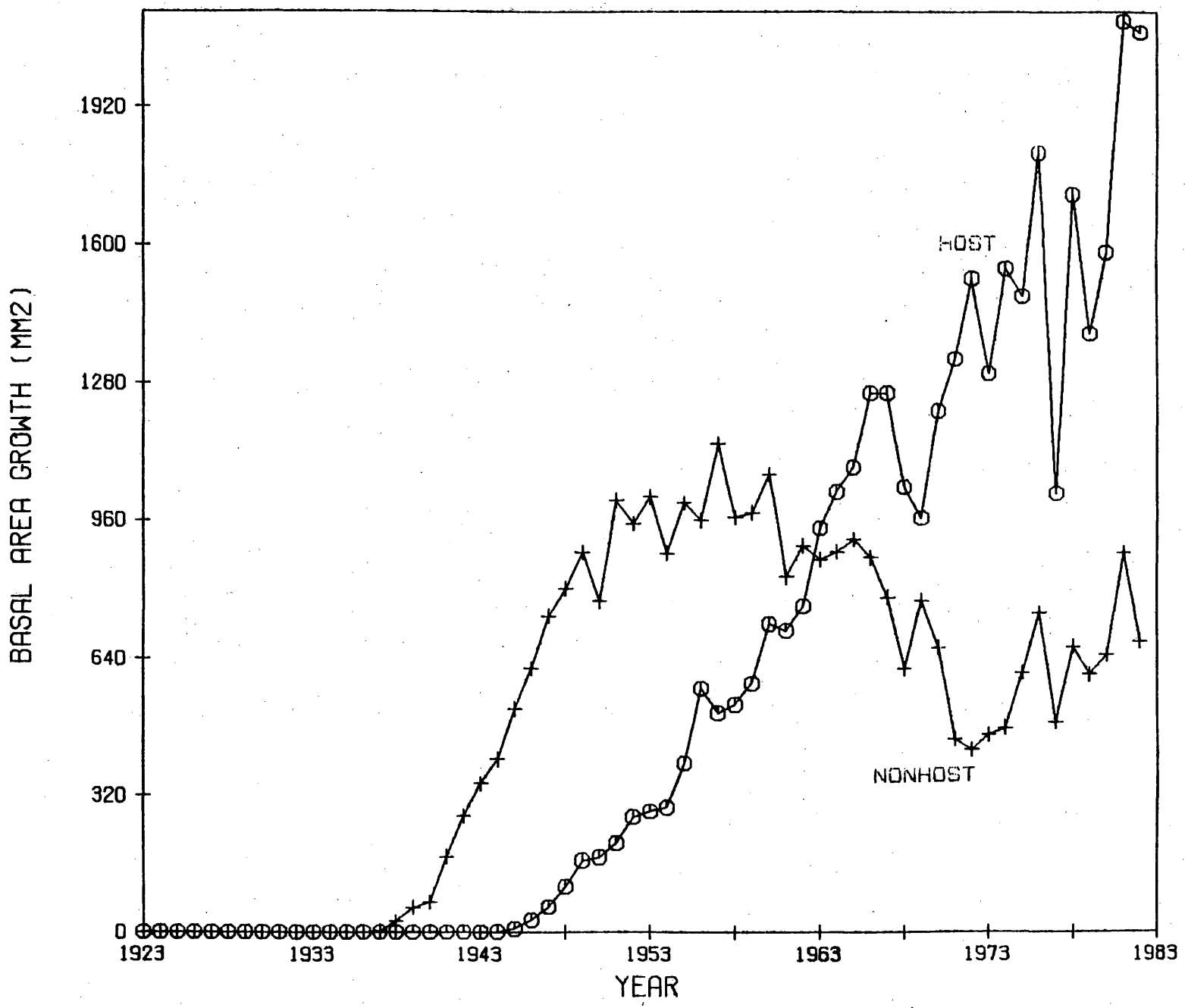

Figure 8. Average BAI by year for two host trees and two nonhost trees from a mixed stand in Area I.

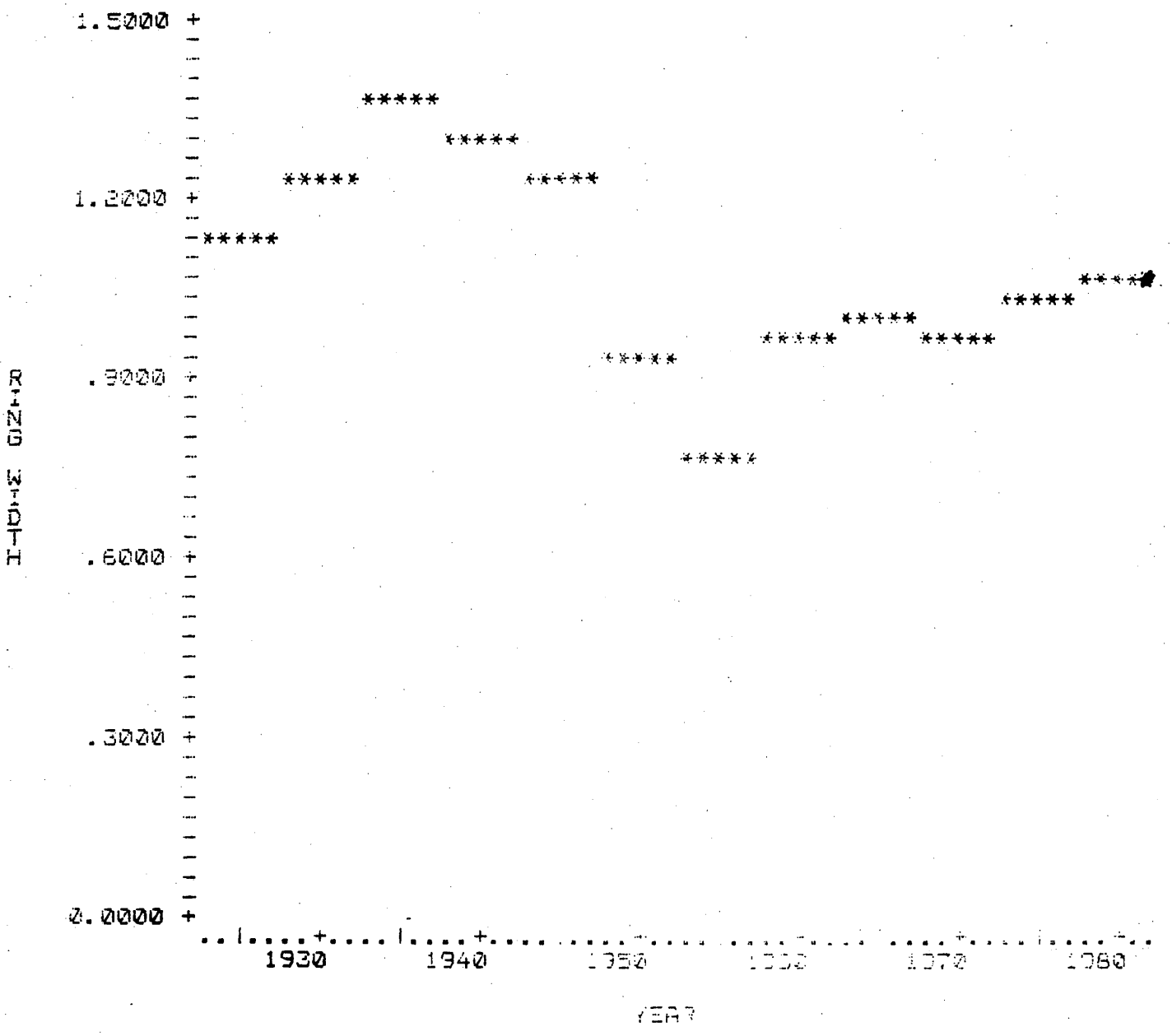

Figure 9. Annual ring widths by five year periods for average of three nonhost trees growing in a mixed host/nonhost stand in Area I.

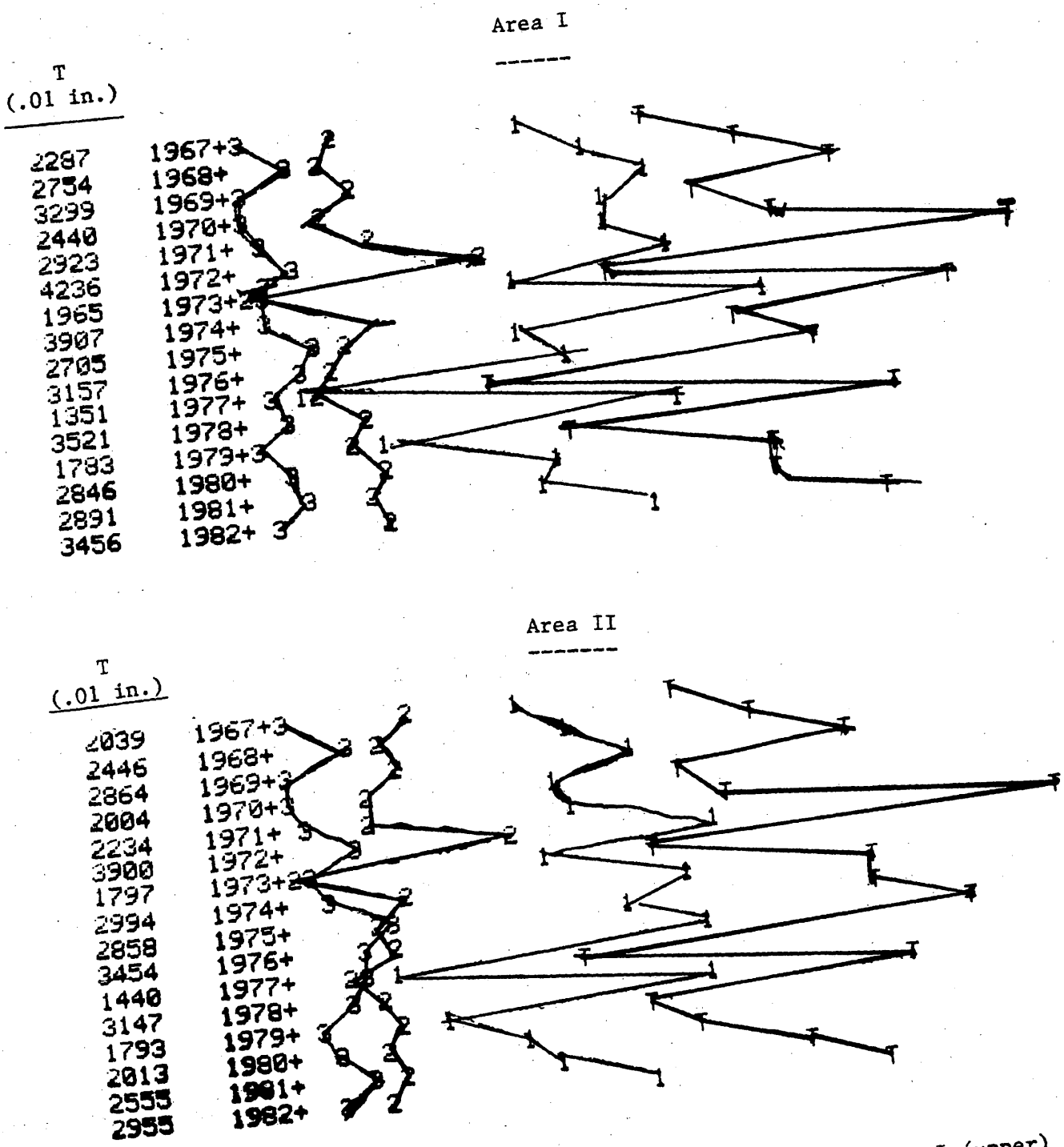

Figure 10A. Periodic precipitation from 1968 to 1982 in Areas I (upper) and II (lower).

Periods:

1 = September$_{(t-1)}$ to January$_{(t)}$

2 = February$_{(t)}$ to April$_{(t)}$

3 = May$_{(t)}$ to August$_{(t)}$

T = May$_{(t-1)}$ to August$_{(t)}$

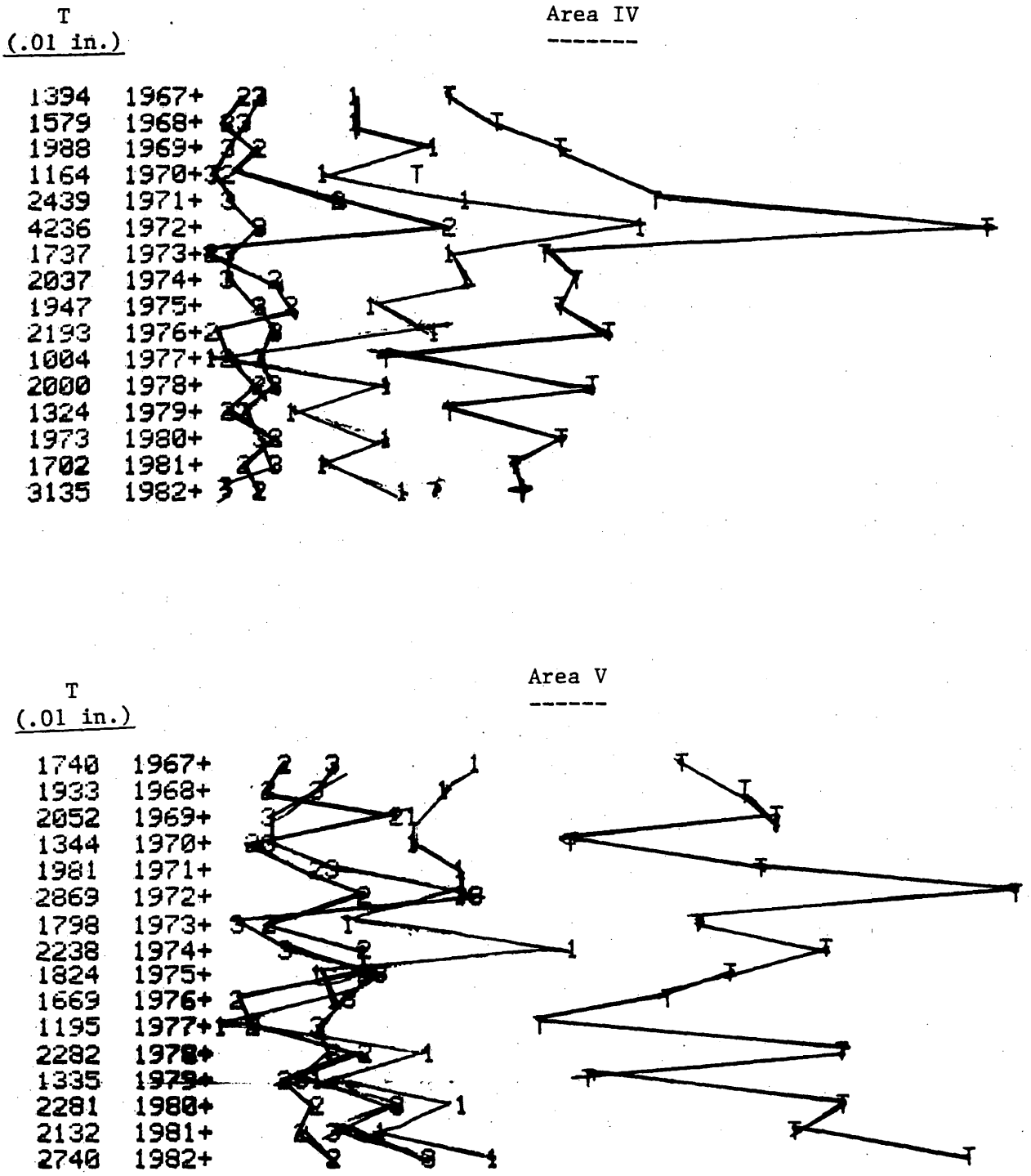

Figure 10B. Periodic precipitation from 1969 to 1982 in Areas IV(upper) and V (lower).

Periods:

1 = September$_{(t-1)}$ to January$_{(t)}$ 2 = February$_{(t)}$ to April$_{(t)}$

3 = May$_{(t)}$ to August$_{(t)}$ T = May$_{(t-1)}$ to August$_{(t)}$

expect these trees to respond quickly to release. Further evidence suggesting that the budworm did not cause the increase is provided by the fact that these trees did not show this increase during earlier budworm epidemics.

No logical explanation for this sudden increase in growth could be found. It is doubtful, however, that weather or the budworm caused this increase. Although the data could still be of some use for predicting seasonal growth, the effect of this sudden increase on the behavior of the cumulative growth models (overestimating predicted growth for the late 1970's to early 1980's) precludes the use of these models.

Another estimate for predicting growth with this data set had to be selected. The method finally chosen is relatively simple, but has a major drawback. For each five year period from 1923 to 1982, BAI of each tree was averaged, and then RBAI was calculated by dividing annual BAI by this average. These proportions were averaged across the 15 nonhost trees for each area, and the results for the period 1977 to 1982 are shown in Table 1. These results are closer to those that were expected, with 1981 and 1982 having higher than average predicted growth rates (RBAI)1.00), which was shown in Figure 1.

Although this method may be adequate for comparing annual growth within a five year period, it requires the assumption that the average of each of the five year periods is equal to some "grand overall average" (e.g. for the sixty year period or some other chosen period). Whether this assumption is correct or not could not be tested with this data, since weather effects could

Table 1. Average RBAI of nonhost trees by area. RBAI calculated by dividing annual growth by five year average.

	AREA				
YEAR	I	II	III	IV	V
1977	1.25	1.10	1.07	.80	.91
1978	1.00	1.00	1.11	.97	1.14
1979	.95	.96	.86	.79	.78
1980	.96	.96	.92	1.09	.99
1981	1.11	1.05	1.10	1.12	1.09
1982	1.02	1.03	1.01	1.02	1.00

not be completely separated from the effects of changing tree conditions due to the anomalous growth patterns noted earlier.

Use of this method also requires the assumption that tree conditions (e.g. competitive relations) do not change greatly within the five year periods. Observations of the growth patterns of the numerous trees in this study revealed that it is reasonably safe to make this assumption. In spite of the drawback of the first assumption, the method for predicting growth appeared to be the best method available under the constraints of the data, so the analysis was continued using this method.

For each of the 194 host trees used for building the defoliation/growth model, relative annual growth was calculated using the five year periods used for the nonhost trees. These proportions were compared to those of the nonhost trees for the years 1923 to 1942 and 1958 to 1972. These periods were chosen because they were determined to be free from the effects of the budworm in all the areas sampled (based on FIDM records and diameter growth patterns).

The relationships between host and nonhost relative annual BAI, averaged for each area, are shown in Figures 11A to 11E. The correlations are suprisingly poor, and the correlations varied somewhat between areas. It should be noted that several transformations of the data were compared, but none had a positive effect on the correlations, and the nontransformed data did not appear to have a nonlinear relationship or a heterogeneous variance, so the nontransformed data was used. In

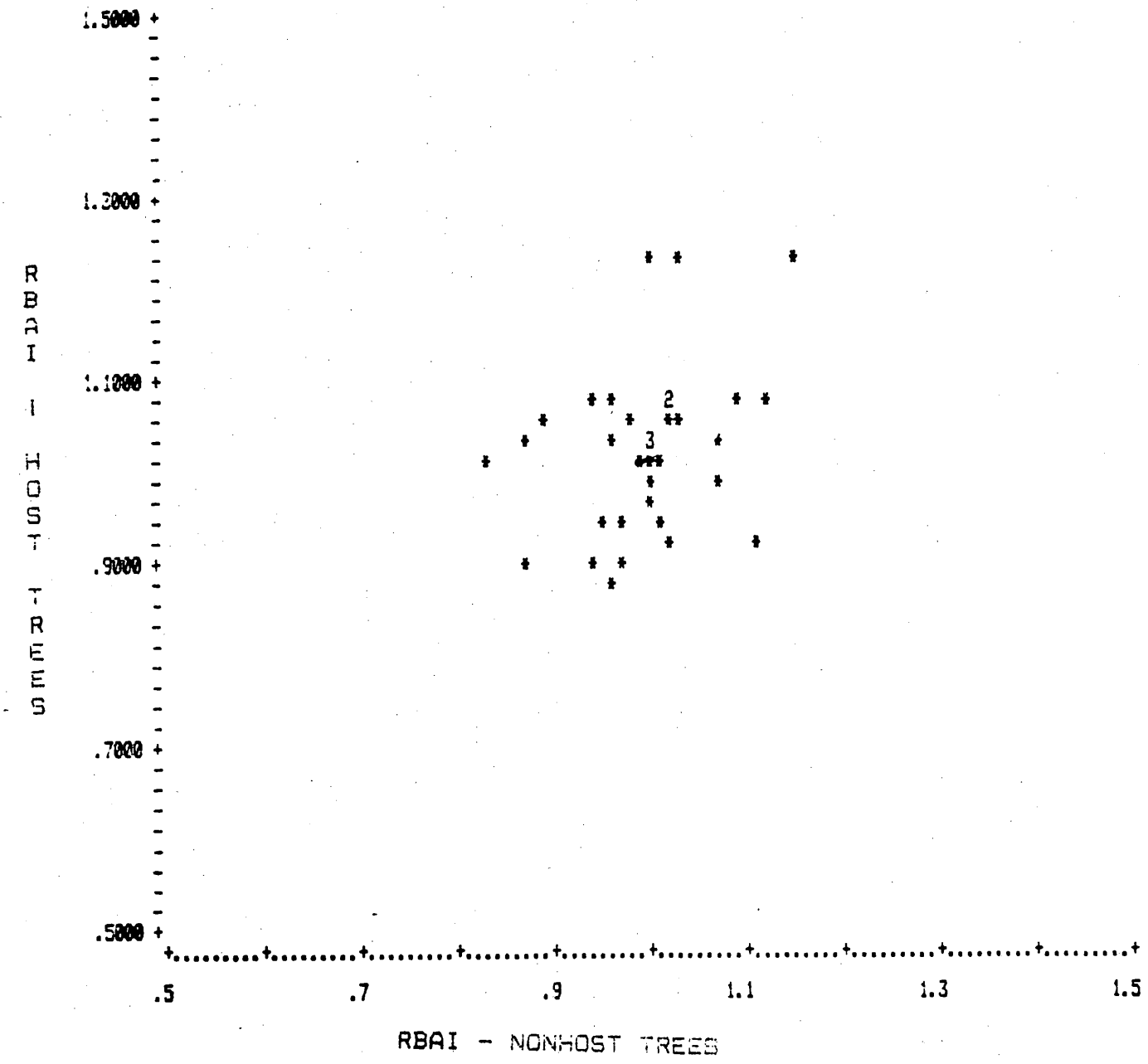

Figure 11A. Average RBAI of host trees versus nonhost trees in Area I. **Numerals refer to multiple points.**

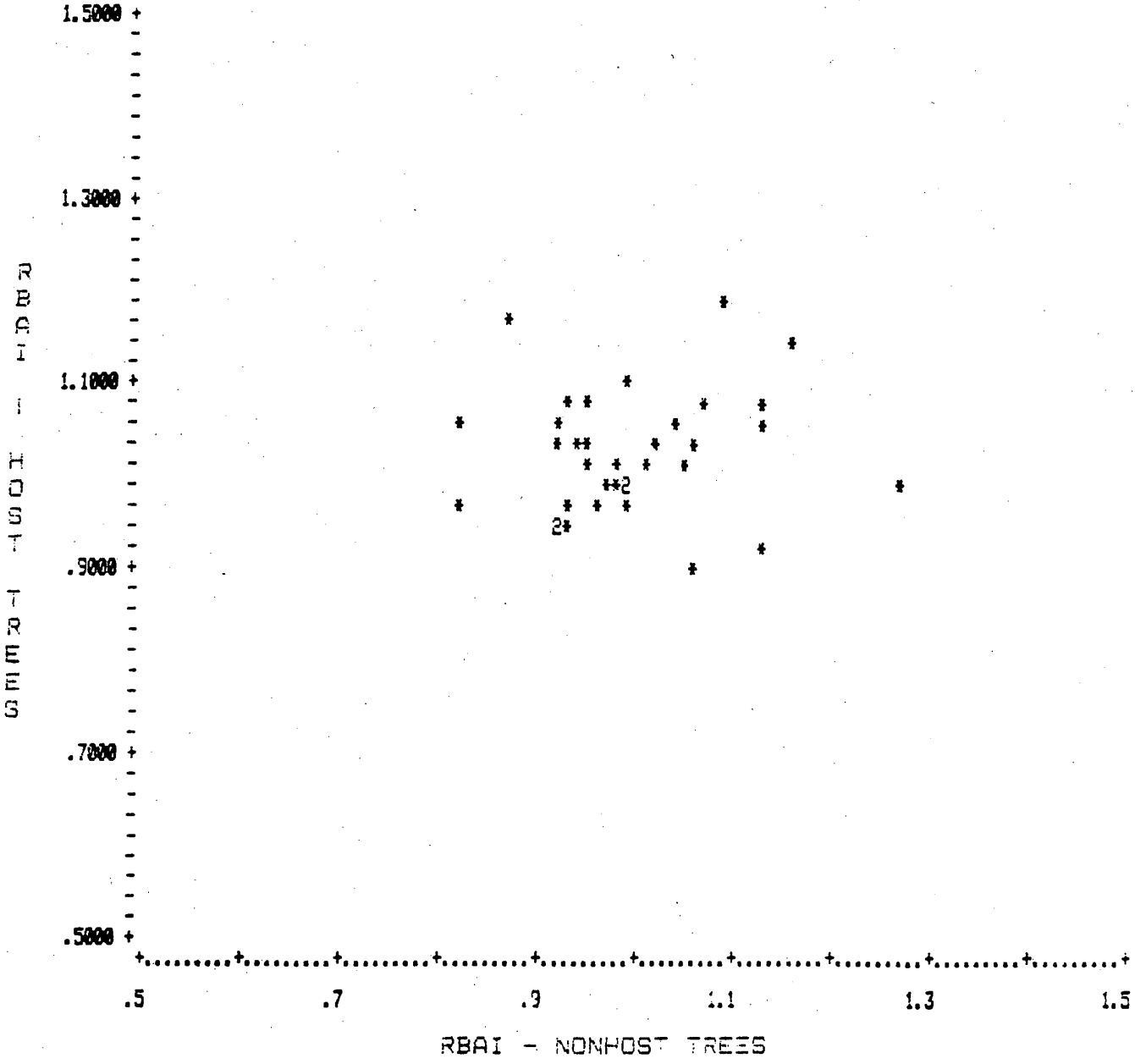

Figure 11B. Average RBAI of host trees versus nonhost trees in Area II.

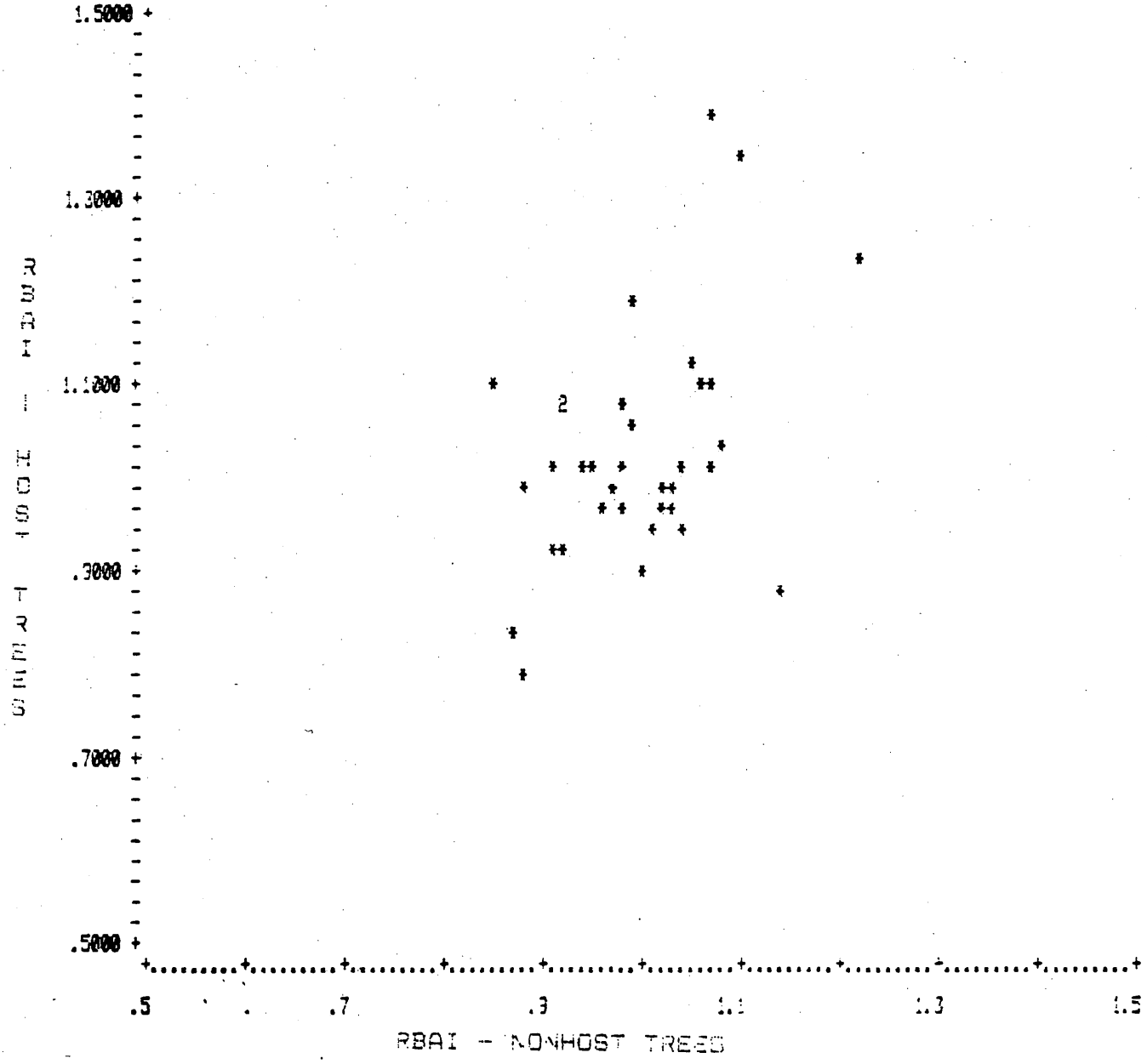

Figure 11C. Average RBAI of host trees versus nonhost tree in Area III.

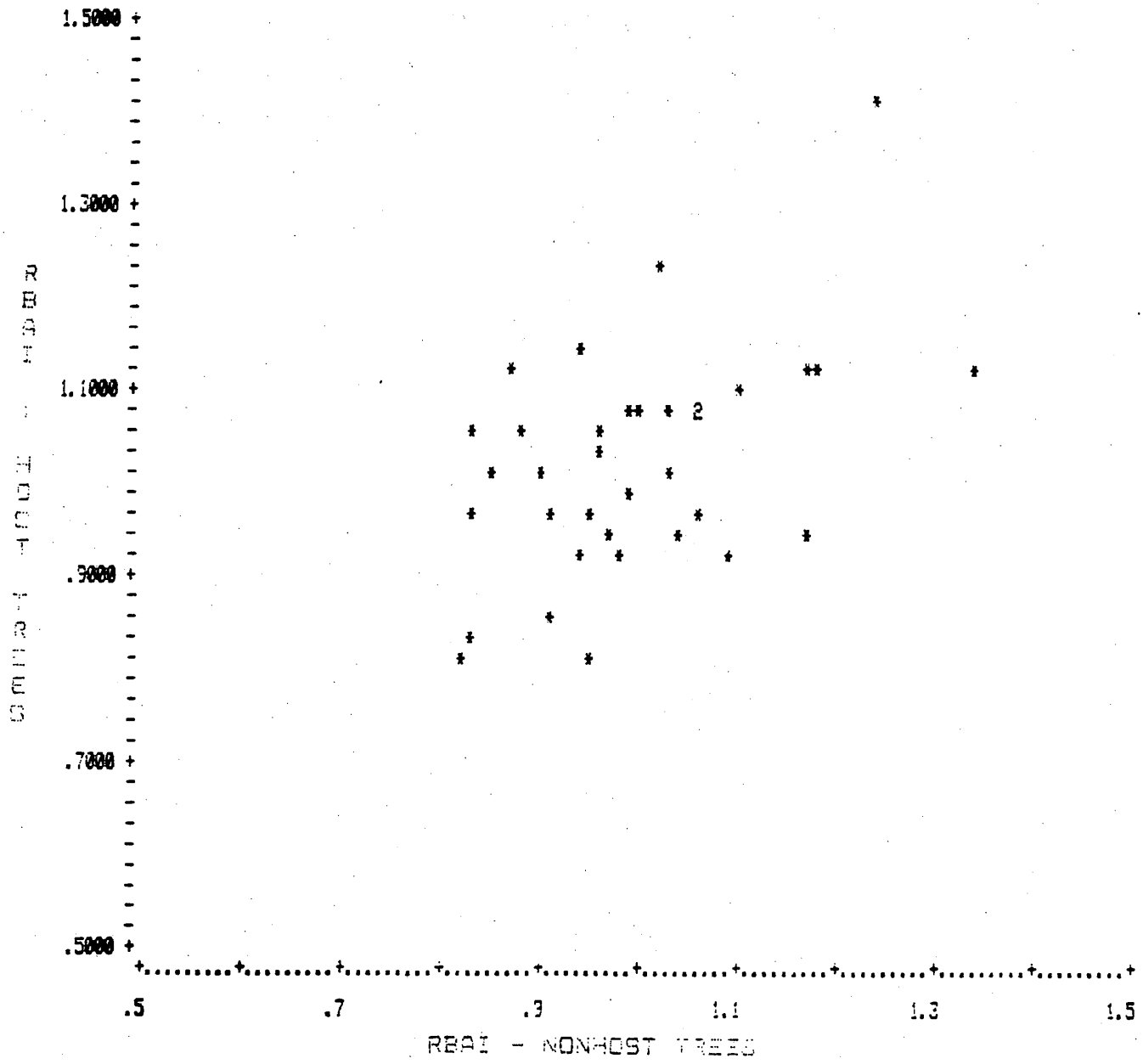

Figure 11D. Average RBAI of host trees and nonhost trees in Area IV.

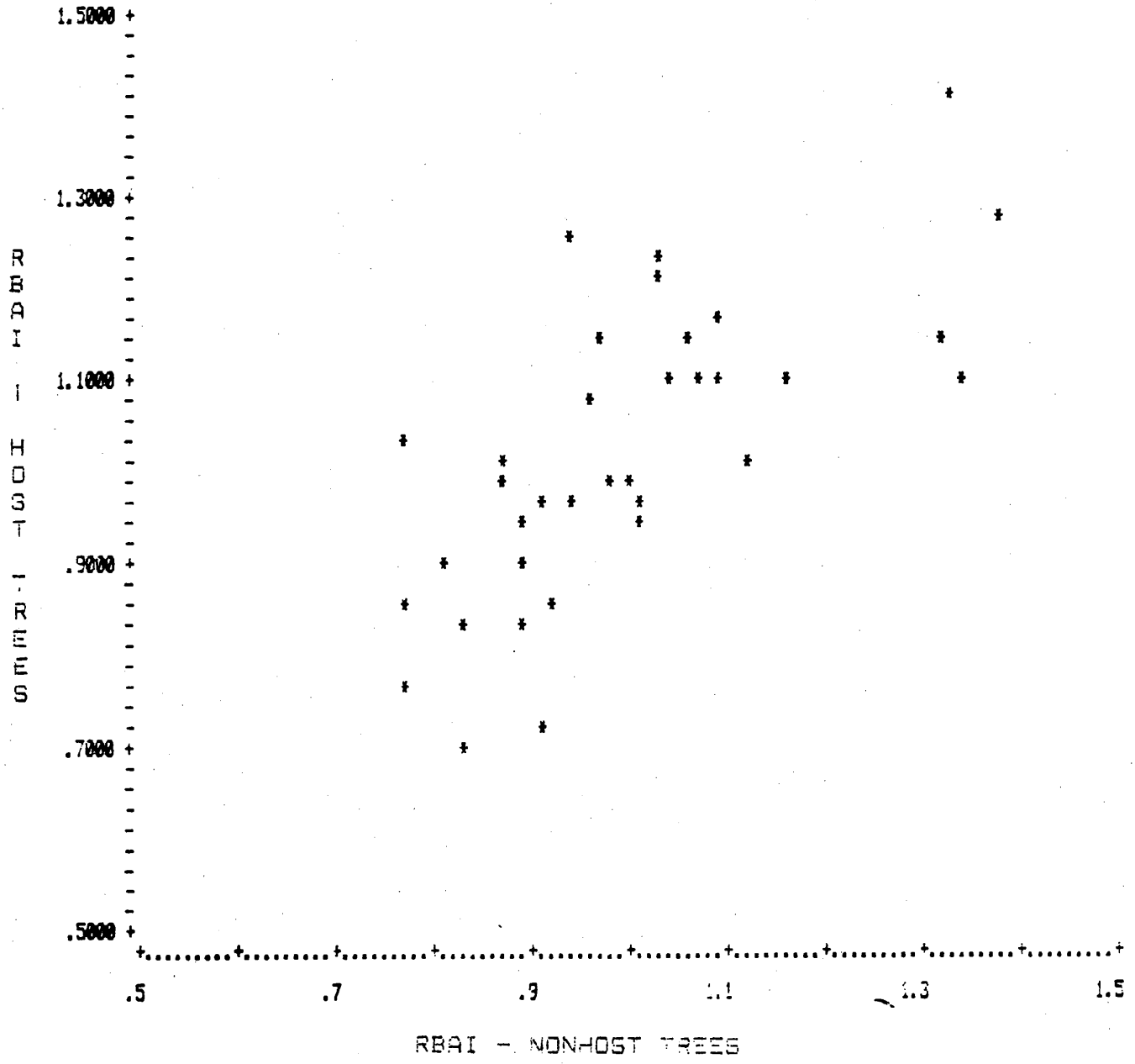

Figure 11E. Average RBAI of host trees and nonhost trees in Area V.

spite of the poor correlations the analysis continued, again because there did not appear to be a better method to use.

For the years 1923 to 1942 and 1958 to 1972, RBAI for each host tree was regressed against the average RBAI of the nonhost trees form the respective area. These individual tree equations were then used to predict annual relative growth for the host trees (RBAIw) for the years 1977 to 1982. Again, there were poor correlation for these equations - the average r-squared value was 0.078 .

The RBAIw values for each tree were multiplied by the predicted diameter squared increment (PDDS - obtained from the Prognosis model) to yield annual estimates of adjusted predicted growth (APDDS) which include individual tree and stand factors (from the Prognosis model) and annual weather effects (from the nonhost tree models). The measured diameter squared increment values (MDDS) were divided by the APDDS values to obtained adjusted relative growth (ARDDS) for each of the years modelled for budworm impact. For most of the trees, these years were 1980 to 1982. On 21 trees, the years 1977 through 1979 were also used, since defoliation of these trees did not start until 1977 and the defoliation records included these years.

With the new estimates of APDDS and ARDDS, regressions between growth and foliage values (RPB = retained proportion of biomass - discussed in the 1983 Scott and Nichols report) were carried out in a manner similar to that used when the unadjusted growth models were developed. To show an estimate of the form of the relationship between ARDDS and RPB, average RDDS was computed

for each 10% RPB class, and the results are shown, along with the regression line, in Figure 12. Figure 13 shows the same averaged estimates for the data using predicted estimates that do not include the adjustments for growing season (RDDS=MDDS/PDDS).

It is apparent that using the adjustments increased the predicted estimates of growth (APDDS), which was expected, resulting in lower relative values (ARDDS=MDDS/APDDS). Most importantly, the adjusted values yielded logical results. When the amount of foliage is 100% of expected, the model predicts growth to be approximately 100% of expected. Using the unadjusted values, growth was predicted to be 121% of expected.

Similar to the models developed in the original project, duration of attack was added to the model. The model fit was:

$$MDDS = A * APDDS^{B1} * (DUREC+1)^{B2} * RPB^{(B3 + B4 * DUREC)}$$

equivalent to:

$$\ln(MDDS)=\ln(A)+B1*\ln(APDDS)+B2*\ln(DUREC+1)+B3*\ln(RPB)+ B4*\ln(RPB)*DUREC$$

where DUREC = number of years of attack less the number of years of recovery. Table 2 lists the coefficients of this model, as well as the model which does not include DUREC. It should be noted that the coefficient for the PDDS term is essentially equal to 1.00, so coefficients for a proportional model (e.g. $\ln(RDDS)=\ln(A)*B2*\ln(RPB)$) would be equal to those of the absolute growth model.

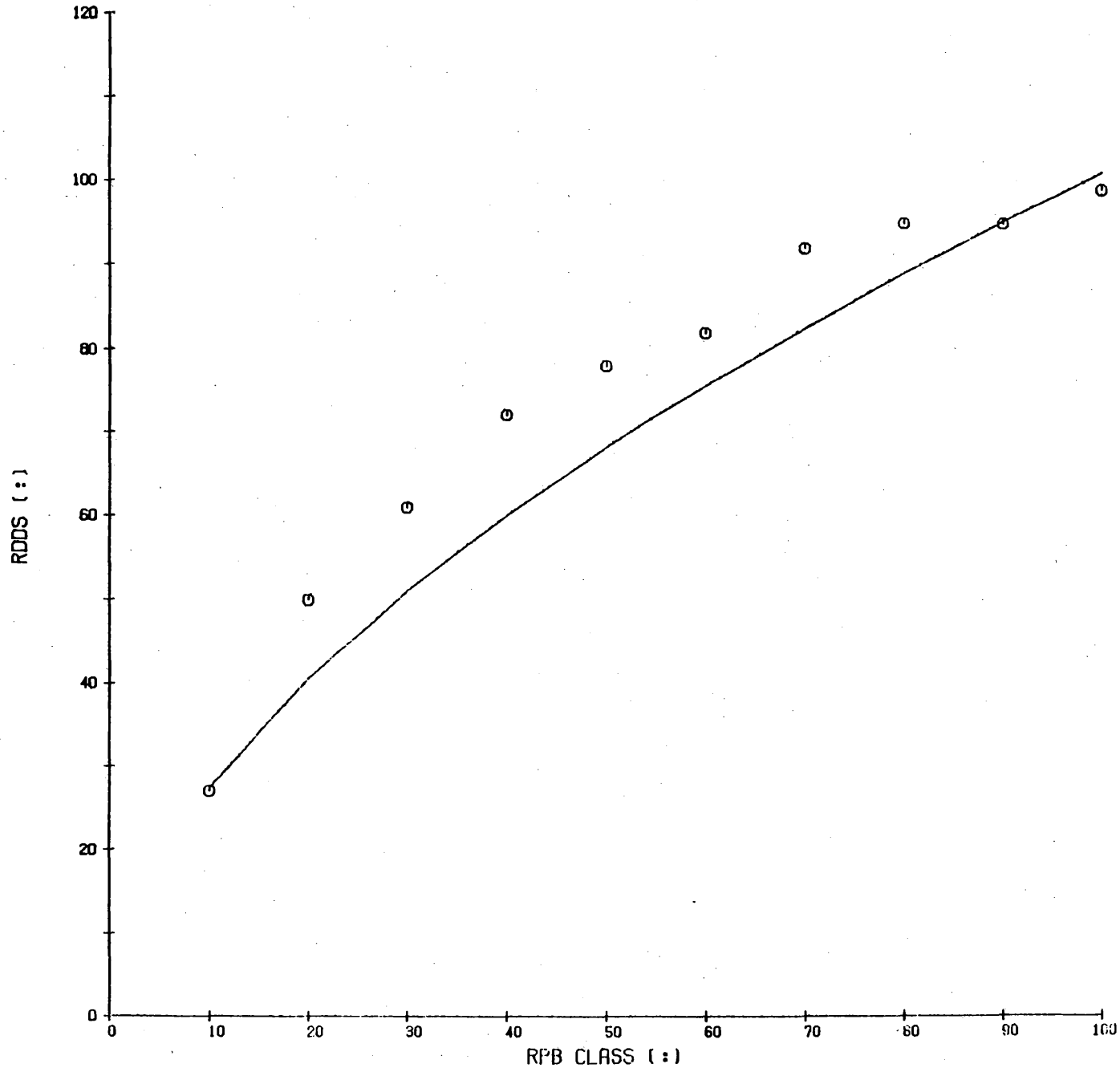

Figure 12. Average RDDS by 10% RPB class, using nonhost correlations to adjust expected growth.

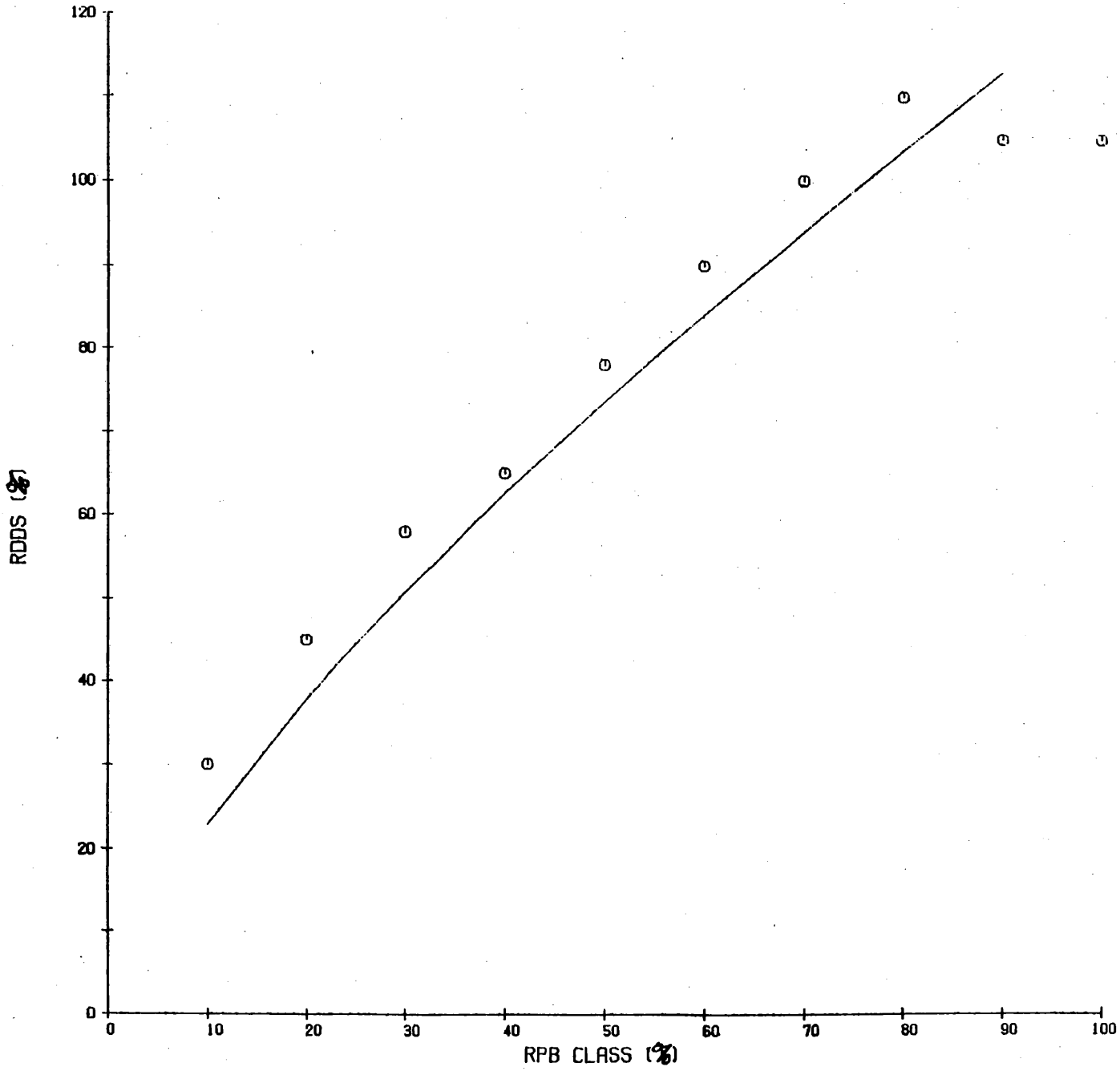

Figure 13. Average RDDS by 10% RPB class, without adjustments for nonhost correlations.

Table 2. Coefficients for models predicting squared diameter increment (ln DDS - $in.^2$) from retained proportion of biomass (RPB) and duration of attack less years of recovery (DUREC), with adjustments for growing season predicted from nonhost tree growth.

VARIABLES	COEFFICIENTS	
ln(PDDS - $in.^2$)	.996259	.995228
ln(RPB%)	.567163	.543452
ln(DUREC+1)		.41466
ln(RPB)*DUREC		-.0486103
Intercept	-2.601	-2.456
R^2	.74	.77

The amount of variance explained using the adjusted values was slightly less than that explained when the unadjusted values were used (R^2 = 0.77 versus R^2 = 0.79). Again, however, the resultant predictions are more logical when the adjustments are used. As seen in Figure 14, the predicted relative growth using the adjusted estimates is close to 100% (105%) when DUREC = 2 and RPB = 100%. With the unadjusted estimates, the predictions are somewhat greater than this (Figure 15).

Although using the nonhost data to adjust for weather gave the desired final results for the models, the poor correlation between nonhost and host tree growth, and the required assumption that the five year periods of growth were all "average", makes one cautious about using the results. For this reason, no attempt was made to use the nonhost diameter growth data to adjust the height increment models.

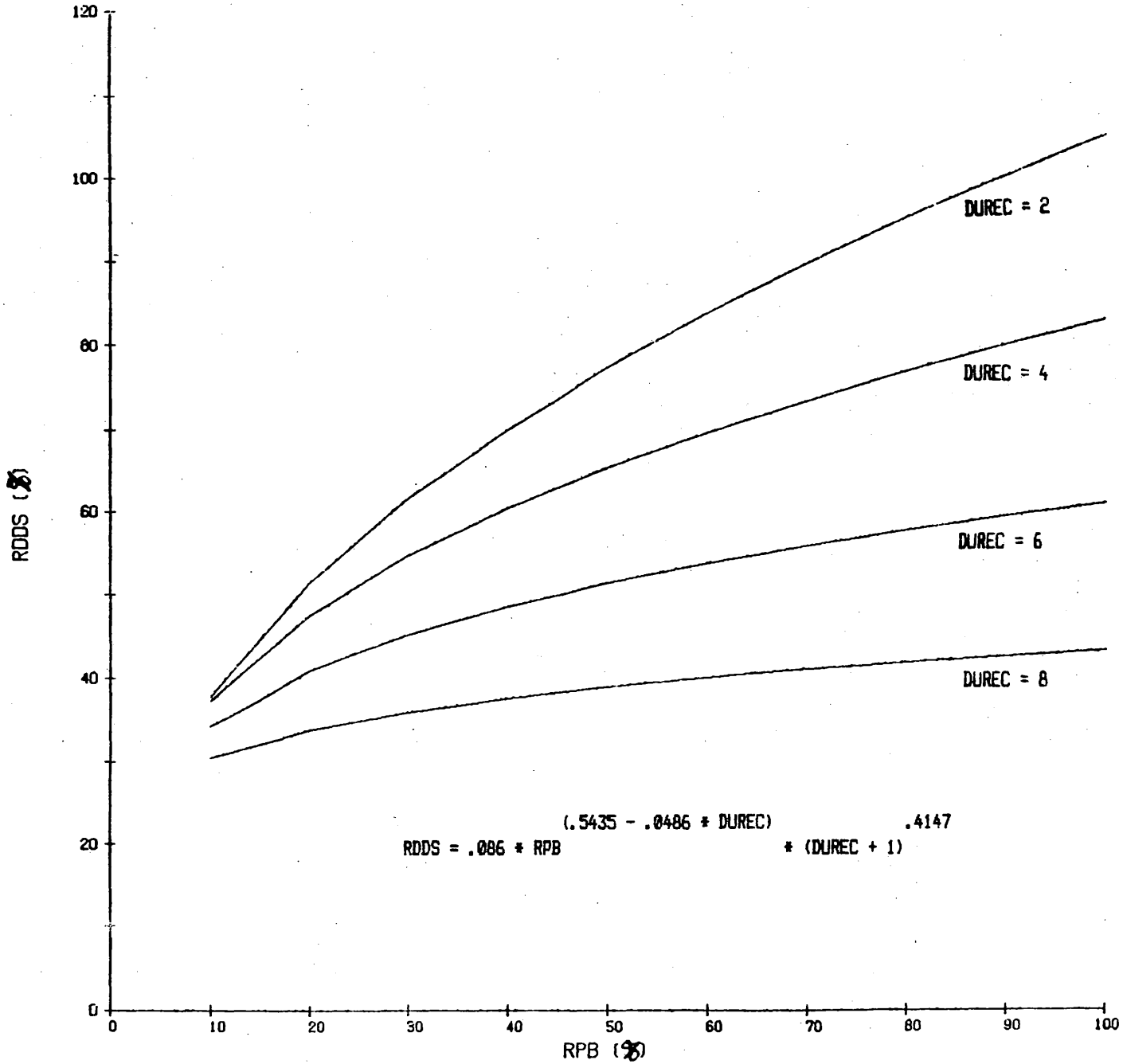

Figure 14. RDDS predicted from RPB and DUREC, using nonhost correlation to adjust expected growth.

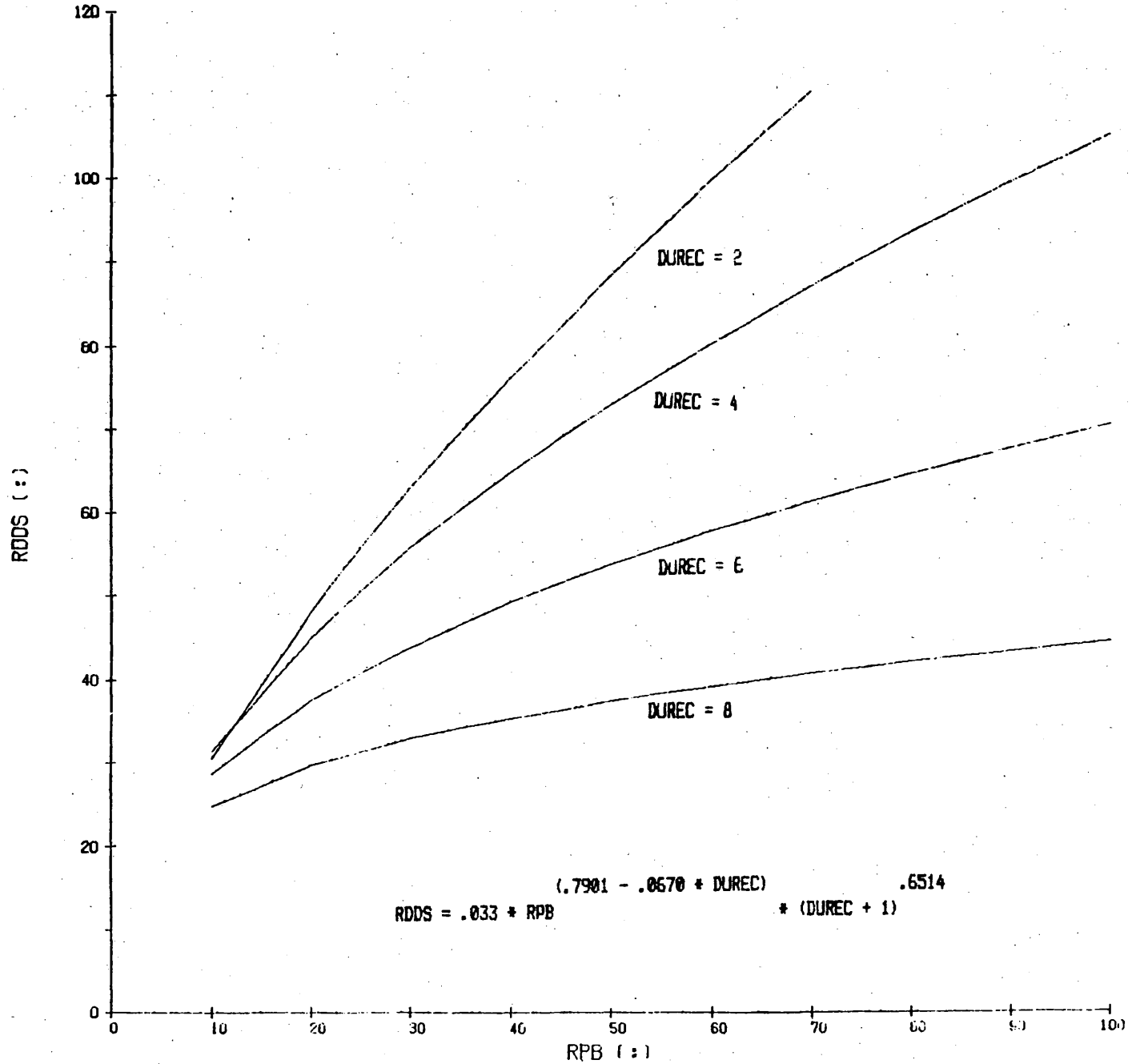

Figure 15. RDDS predicted from RPB and DUREC, without adjustments for nonhost correlation.

********* WEATHER CORRELATION CALIBRATION *********

METHODS AND PROCEDURES

The method selected for using weather variables to predict annual growth was introduced by Zahner and Stage (1966). For a thorough discussion of this method, the reader is referred to their original article. In short summary, the method takes daily precipitation and temperature values, predicts potential soil evaporation, predicts actual soil evaporation (based on soil moisture characteristics and potential evaporation), then computes "moisture stress", defined as the difference between potential and actual evaporation.

Fortunately, CANUSA had already funded a major research program using daily weather data, so little keypunching of weather data was required. This data was supplied by Dr. Bill Kemp, University of Idaho.

Moisture holding abilities of the soils on each site were also needed for the program to predict moisture stress. The field and laboratory data necessary for this were collected by Dr. Ula Moody (1983). A summary of Dr. Moody's data, showing available moisture in the rooting zone at various soil moisture tensions, is shown in Table 3.

Table 3. Rooting zone moisture holding capacities of sample sites - summary of data from Moody (1983).

STAND	ROOT DEPTH	COARSE-NESS	MOISTURE HOLDING CAPACITY (in.) atm.						AVAILABLE WATER
	(in.)	(%)	1/3	2/3	1	2*	5	15	(in.)
1	25	51	2.14	1.71	1.36	1.27	1.09	1.20	0.94
2	30	62	2.33	1.86	1.48	1.48	1.20	1.31	1.03
3	30	13	4.46	3.11	2.69	2.47	2.32	2.12	2.34
4	48	37	3.08	2.52	1.99	1.94	1.85	1.84	1.24
5	50	0	9.43	7.19	5.42	5.05	4.58	4.49	4.94
6	35	23	3.42	2.99	2.30	2.15	2.01	2.05	1.38
11	36	44	3.91	3.13	2.50	2.31	2.01	1.81	2.10
15	36	45	1.45	1.18	0.87	0.83	0.86	0.63	0.82
16	30	8	1.82	1.49	1.02	1.00	1.17	0.87	0.95
17	32	3	8.47	6.04	4.60	3.98	3.57	2.83	5.64
18	32	11	6.88	5.76	4.50	4.22	3.82	3.08	3.80
20	36	28	3.29	2.46	1.78	1.65	1.64	1.33	1.97
21	40	3	5.20	4.20	3.23	3.33	2.44	2.09	3.11
22	38	62	3.42	2.84	2.17	2.08	1.97	1.65	1.78
23	30	39	5.35	4.08	3.59	3.34	3.05	2.76	2.58
25	36	66	3.04	2.36	1.87	1.84	1.68	1.48	1.56
28	48	1	15.56	13.86	12.41	11.67	10.50	10.19	5.37
29	32	2	8.55	7.03	5.79	5.30	4.45	4.26	4.29
30	22	4	5.84	4.62	3.58	3.31	3.00	2.73	3.11
31	36	62	2.99	2.44	2.16	1.93	1.68	1.76	1.23
34	30	34	3.54	2.70	2.35	2.18	1.82	1.52	2.01
35	48	37	3.87	3.28	2.65	2.50	2.39	2.10	1.76
39	44	34	6.85	5.13	4.07	3.57	3.09	3.05	3.80
44	26	14	6.31	4.60	3.79	3.39	2.76	2.06	4.24
46	48	8	7.80	6.05	4.71	4.30	3.27	3.16	4.64
47	24	0	7.41	5.49	4.65	4.20	3.45	3.31	4.10

* Values at 2 atmospheres obtained by handfitting curves to soil moisture release curves.

ANALYSIS, RESULTS AND DISCUSSION

It should be noted that the values reported for moisture holding capacity in Table 3 appear to be quite low. When first observed, these were low enough to warrant checking into the methods used. These methods, however, are standard practice. When this was discussed with Dr. Moody, she was not surprised to hear of the low calculations of soil moisture holding capacities. Soils on these sites were some of the most drought-prone she has worked on. Textures of the soil particles were not the major cause of the low moisture holding abilities of these sites. Instead, the combination of high rock contents (decreasing the amount of soil available for water storage) and shallow rooting depths, as shown in Table 3, causes the droughty nature.

The finding of low soil moisture holding abilities on these sites suggests possibilities for further research. Fauss and Pierce (1969) found that stands in the Rocky Mountains on drier sites had higher budworm defoliation rates than those on wetter sites. Since moisture holding abilities in the rooting zones on the sites in the present study is also quite low, this parameter could be useful in a model predicting site susceptibility to spruce budworm infestation. One might take this a step farther and add the effects of climate by calculating an average annual moisture stress for a site (using Zahner and Stage's program).

This is beyond the scope of the present study, but could be useful in future studies.

Weather data from the closest weather station was obtained for each of the five geographical areas in this study. Depending on the station, days or months of weather data were missing, so predictions were needed for the missing data. From the methods studied by Kemp et al (1983), it appeared that the best method to use with this data set was a method using data from nearby stations in a regression equation.

The equation used for predicting missing temperatures was:

$$T_{i,J} = \sum_{x=1}^{2} \left(W_{i,x} * (A_{i,x} + B_{i,x} * T_{x,J}) \right)$$

$T_{i,J}$ = temperature at station 'i' on day 'J'

$T_{x,J}$ = temperature at station 'x' on day 'J'

$A_{i,x}$ and $B_{i,x}$ = coefficients from the equation predicting temperature at station 'i' from data at station 'x'

$W_{i,x} = r^2_{i,x} / (r^2_{i,x} + r_{i,y})$

where $r^2_{i,x}$ and $r^2_{i,y}$ are coefficients of determination for equations predicting data at station 'i' from stations 'x' and 'y'.

Data from two additional weather stations was added to the data set of five original stations for these predictions. Names of weather stations, distances to the drainages, and the names and distances of stations used for predictions are shown in Table 4. Missing precipitation data was handled in the same manner, except ln-ln models were used. Between-station relationships of temperature were high (r^2 = 0.88 to 0.97), while those of precipitation were lower (r^2 = 0.55 to 0.75).

Before daily values were calculated, some adjustments were made to the computer program predicting moisture stress. Since the sites monitored in this study were always at higher elevations than the weather stations, corrections to the temperature measurements were needed. These were made by adding a function which multiplied the dry adiabatic lapse rate (5.5°F/1000 ft.) by the difference in elevation between the site and the weather station.

Another change to the program was made in the way it handled calculations of soil moisture holding capacity at 2 atmospheres (this is the tension at which the program predicts soil moisture stress to begin occurring). The program uses an external function for this, and the user chooses different functions depending on a general soil texture description. Instead of using values given in the program for the general soil descriptions, calculated values of moisture holding capacity from the collected data were used. Since soil texture on all of the sites studied was similar, the form of the function stayed the same.

Table 4. Elevations and distance from sites to weather stations.

	AREA				
	I	II	III	IV	V
Average Elevation of Area (ft.)	3600	3150	3200	2800	3800
Primary Weather Station	C	A	D	G	E
Distance to Station (mi.)	5	8	3	10	3
Station Elevation (ft.)	1128	1930	1940	1755	2320
Predicting Station 1	D	C	C	E	G
Distance to Station	15	11	9	22	20
Predicting Station 2	B	D	B	F	F
Distance to Station	14	25	5	11	27

- -

Station A = Cle Elum

Station B = Lake Wenatchee

Station C = Leavenworth

Station D = Plain

Station E = Conconully

Station F = Mazama

Station G = Winthrop

Sites within each drainage having similar moisture holding capacities and elevations were pooled prior to running the program. Nineteen separate combinations of moisture capacity and elevation were identified. Moisture stress was calculated from Julian day 91 (April 1) to Julian day 290 (October 17) for each combination each year from 1957 to 1982. It was assumed that these days included the periods that could affect growth (in most cases, it probably exceeded the periods of growth).

The model used to predict annual growth was based on the design of Zahner and Stage (1966). Instead of using deviation from average growth as the dependent variable, however, proportion of predicted growth was used. Predicted growth was the same as that used in the earlier section (Nonhost Correlation). For the calibration period (1958 to 1972), predicted growth was average five-year growth, while for the modeled period (1973 to 1982), estimates using the Prognosis model were used.

Fifth order polynomial models were fit between moisture stress and Julian day for the 200-day period each year. Similar models were fit for temperature and precipitation. Coefficients from these models were used as independent variables in the models predicting proportion of predicted growth. In addition, proportional growth in the previous year was also used, as well as the coefficients from the polynomial models in the previous year.

The complete model tested was:

$$Y_i = B_1 * Y_{i-1} + B_2 * S_i + B_3 * T_i + B_4 * P_i + B_5 * S_{i-1} + B_6 * T_{i-1} + B_7 * P_{i-1}$$

Y_i = proportional growth in year 'i'

B2 to B6 each represent sums of the six coefficients describing weather factors - for example:

$$B_2 * P_i = B_{2,1} * P_{i,1} + B_{2,2} * P_{i,2} + \ldots + B_{2,6} * P_{i,6}$$

$P_{i,1}$ = first coefficient from the fifth degree polynomial in year 'i'

S = moisture stress

T = temperature

P = precipitation

For each of the 26 stands, models for both basal area and height increment were fit. None of the terms above the third power of the polynomials were significant (Zahner and Stage found significant terms through the fourth power). The models including the significant terms were then used to predict proportional growth for the years 1977 to 1982 for each of the stands, and the results are shown in Tables 5 and 6. These models

Table 5. Proportional diameter squared increment predicted from weather variables by stand for the years 1977 to 1982.

	YEAR					
STAND	1977	1978	1979	1980	1981	1982
1	.96	1.04	.88	1.03	1.22	1.10
2	.98	.95	1.01	1.00	1.28	1.04
3	1.04	1.00	.92	.98	1.13	1.00
4	1.01	.92	.92	.94	1.10	1.01
5	.92	.99	.98	1.00	1.14	.99
6	.97	1.00	.94	.96	1.09	1.04
11	.85	1.01	.82	1.06	1.18	1.04
15	.74	1.06	.72	.92	1.10	1.02
16	.78	1.02	.71	.88	1.15	1.09
17	.82	1.08	.75	.94	1.09	1.15
18	.76	1.04	.75	.92	1.18	1.08
20	.74	1.00	.70	.85	1.10	1.12
21	.74	1.00	.70	.85	1.10	1.12
22	.90	.98	.99	.98	1.15	1.09
23	.91	1.01	.94	.98	1.08	1.07
25	.96	.98	.98	.97	1.12	1.04
28	1.01	1.06	.94	.98	1.08	1.03
29	.99	1.02	.98	.97	1.11	1.00
30	.74	1.02	.72	1.03	1.12	1.04
31	.81	.94	.77	1.00	1.16	1.10
34	.76	.97	.82	1.04	1.10	1.10
35	.79	1.01	.80	1.04	1.08	1.04
39	.84	.97	.78	1.00	1.09	1.08
44	.88	1.04	.76	.92	1.28	1.05
46	.92	1.06	.72	.86	1.29	1.14
47	.86	1.01	.75	.87	1.20	1.13

Table 6. Proportional height increment predicted from weather variables by stand for the years 1977 to 1982.

	YEAR					
STAND	1977	1978	1979	1980	1981	1982
1	.962	1.065	.918	1.027	1.191	1.052
2	.955	.979	1.015	.952	1.283	1.015
3	1.084	.979	.936	.955	1.079	.966
4	.967	.909	.876	.962	1.133	1.021
5	.904	.948	.992	.983	1.149	.968
6	.923	1.045	.934	.973	1.067	1.050
11	.832	.988	.801	1.064	1.226	1.006
15	.734	1.048	.732	.907	1.122	1.042
16	.796	1.037	.722	.889	1.137	1.072
17	.854	1.118	.786	.986	1.110	1.103
18	.742	1.025	.714	.897	1.169	1.061
20	.737	1.019	.722	.834	1.092	1.173
21	.742	1.014	.680	.845	1.146	1.130
22	.863	.989	1.000	.984	1.139	1.066
23	.901	1.040	.965	.961	1.079	1.038
25	.947	.959	.975	.977	1.118	1.078
28	1.014	1.063	.976	.997	1.050	1.010
29	1.000	.987	.988	.988	1.134	.957
30	.740	.973	.746	1.025	1.171	1.036
31	.833	.896	.791	.958	1.166	1.126
34	.763	.923	.796	1.056	1.148	1.107
35	.789	.994	.784	1.088	1.113	1.075
39	.801	.991	.798	1.050	1.142	1.031
44	.912	1.090	.782	.952	1.308	1.064
46	.921	1.007	.729	.841	1.336	1.194
47	.851	.967	.755	.844	1.181	1.146

had much better fits than the nonhost correlation models, on the average explaining 65% of the variation in proportional diameter growth and 47% of the variation in proportional height growth (the nonhost models explained 8%).

In the same manner used in the nonhost correlation analysis, predicted height and diameter squared growth (from the Prognosis model) for the years 1977 to 1982 was multiplied by the predicted proportional growth (from the weather models) to produce adjusted predicted growth (APDDS = adjusted predicted change in squared diameter, APHTI = adjusted predicted height increment).

These adjusted values were used to recompute the models predicting growth from foliage and attack duration. Coefficients for the new models are shown in Table 7. Similar to the earlier models, the computed exponents for the APDDS and APHTI terms are essentially equal to 1.00, so these models predicting absolute growth can be used to predict proportional growth by placing APDDS and APHTI on the left side of the equation (MDDS=PDDS*... ; RDDS=MDDS/PDDS=...). The behaviors of the models can be seen in Figures 16 and 17. As expected after the findings in the nonhost analysis, the new models show a decrease over the original models in the predictions of growth at given levels of RPB and DUREC (i.e., growing seasons in the modelled years were predicted to be better than average).

R-squared values for the new models are essentially the same as those of the original models. The proportions of diameter and height growth explained by the new models are 78% and 49% respectively, while those of the original models were 79% and

Table 7. Coefficients for models predicting squared diameter increment (ln DDS - in^2.) and height increment (ln HTI - ft.) from retained proportion of biomass (RPB) and duration of attack less years of recovery (DUREC), with adjustments for growing season predicted from weather variables.

	DDS	HTI
ln(PDDS - $in.^2$)	.99842	
ln(PHTI - ft.)		1.01684
ln(RPB%)	.61240	.43800
ln(DUREC+1)	.44733	-.04761
ln(RPB)*DUREC	-.05306	-.01221
Intercept	-2.784	-1.866
R^2	.784	.492

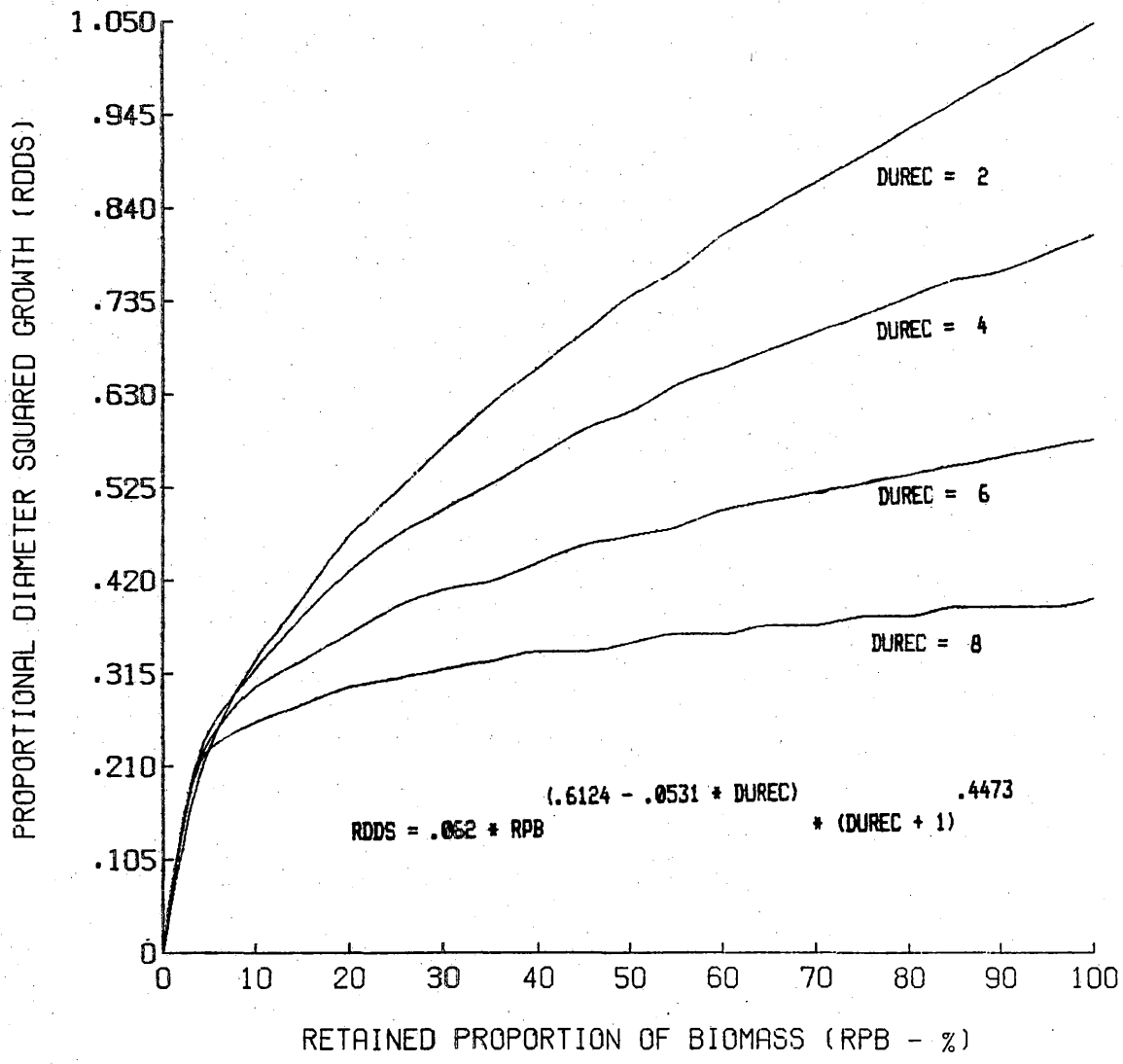

Figure 16. RDDS predicted from RPB and DUREC, using weather variables to adjust predicted growth.

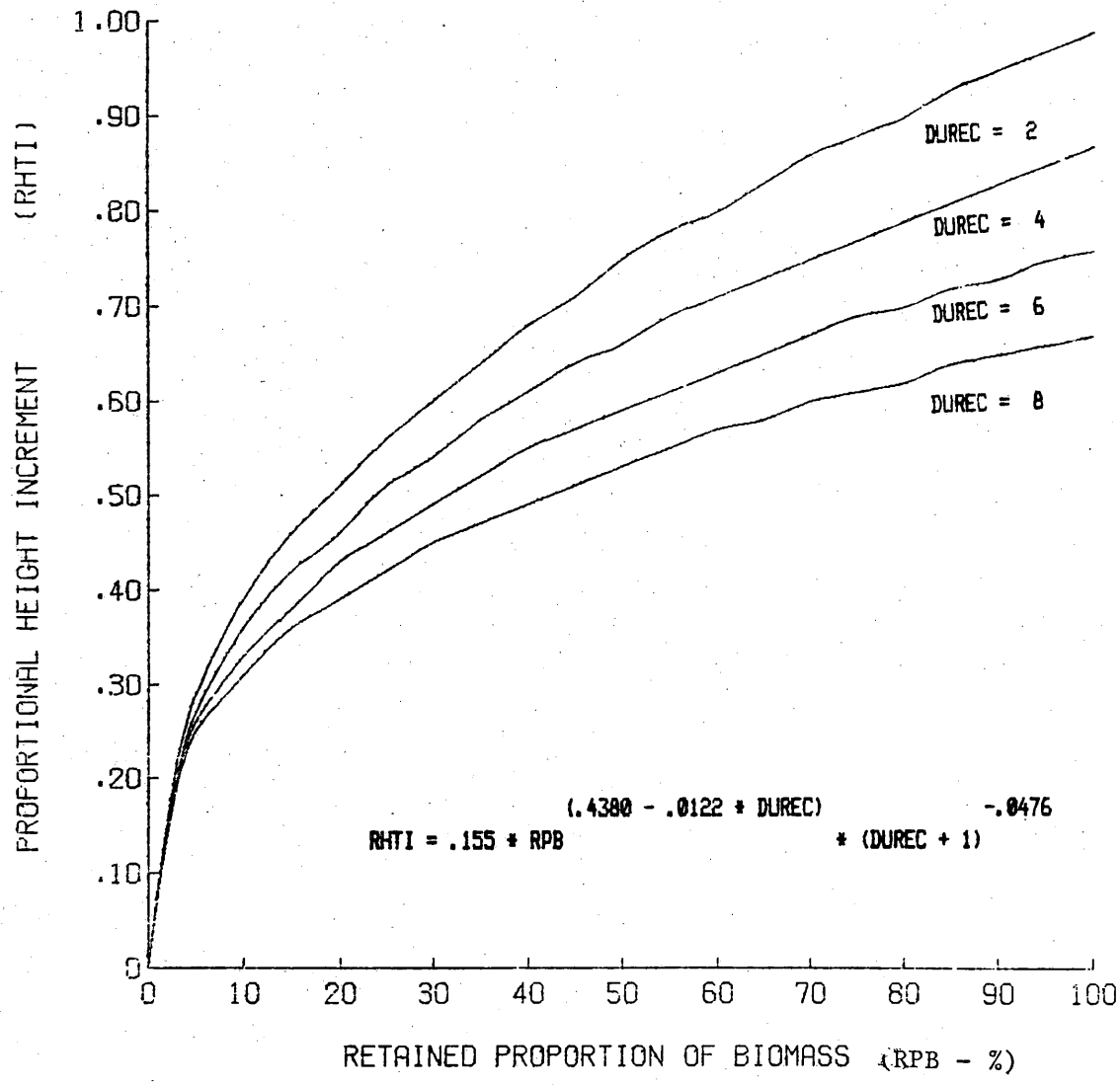

Figure 17. RHTI predicted from RPB and DUREC, using weather variables to adjust expected growth.

49%. As with the nonhost correlation analysis with diameter growth, however, the results of the new models appear to be much more logical.

It is interesting to note the similarity between the diameter growth model computed using nonhost correlation (Table 2 and Figure 14) and the model computed using weather factors. Although the poor correlation between nonhost and host tree growth made one hesitant to use this method, the results from this method are very close to those obtained using the weather models method. If nothing else, they substantiate the results of the weather models analysis.

Another set of models was also computed, using a different term to describe defoliation history. It was noted earlier (Scott and Nichols 1983) that use of the DUREC term (number of years of attack less number of years since attack ended) may limit the use of the models to sites where defoliation levels are similar to those found in the present study. In some instances, budworm levels can build explosively, and the trees may suffer much greater levels of defoliation in the initial stages of the attack. The stand studied by Alfaro et al (1982) is an example of this. From their defoliation and growth data, it is apparent that defoliation levels were much higher in the early stages of the epidemic in their study than they were in the present study. It is also apparent that growth at various levels of defoliation in their stand is much lower than that predicted from the models developed in the present study. Another measure of defoliation

history could improve the present model, but it has to be available from the data set in the present study.

The variable eventually chosen was proportional growth in the previous year. This variable should reflect the effects of prior defoliation on growth in previous years, thereby reflecting defoliation history. Similar to calculating proportional growth in the present year, predicted proportional growth in the previous year (RDDSM1 and RHTIM1) was calculated by dividing the measured growth in the previous year by the predicted growth (adjusted for weather).

Although not a problem when computing the models, it should be noted that use of this value may sometimes cause problems when the models are used. Since predicted growth in one year is dependent upon predicted growth in the previous year, errors in the prediction could be compounded when predicting growth for a number of years.

The results of models fit using proportional growth in the previous year in place of DUREC are shown in Table 8 and Figures 18 and 19. Like the other models fit using adjustments for weather, the models give logical results. These models explained 91% of the variation in diameter growth and 61% of the variation in height growth, which is substantially higher than that explained by the models using the DUREC term.

Table 8. Coefficients for models predicting squared diameter increment (ln DDS - in^2.) and height increment (ln HTI - ft.) from retained proportion of biomass (RPB) and proportional growth in the previous year (RDDSM1 and RHTIM1), with adjustments for growing season predicted from weather variables.

	DDS	HTI
ln(PDDS - $in.^2$)	.99102	
ln(PHTI - ft.)		1.00131
ln(RPB%)	.47252	.38139
ln(RDDSM1)	.32413	
ln(RPB)*RDDSM1	.07000	
ln(RHTIM1)		.55092
ln(RPB)*RHTIM1		-.02120
Intercept	-2.4786	-1.645
R^2	.908	.612

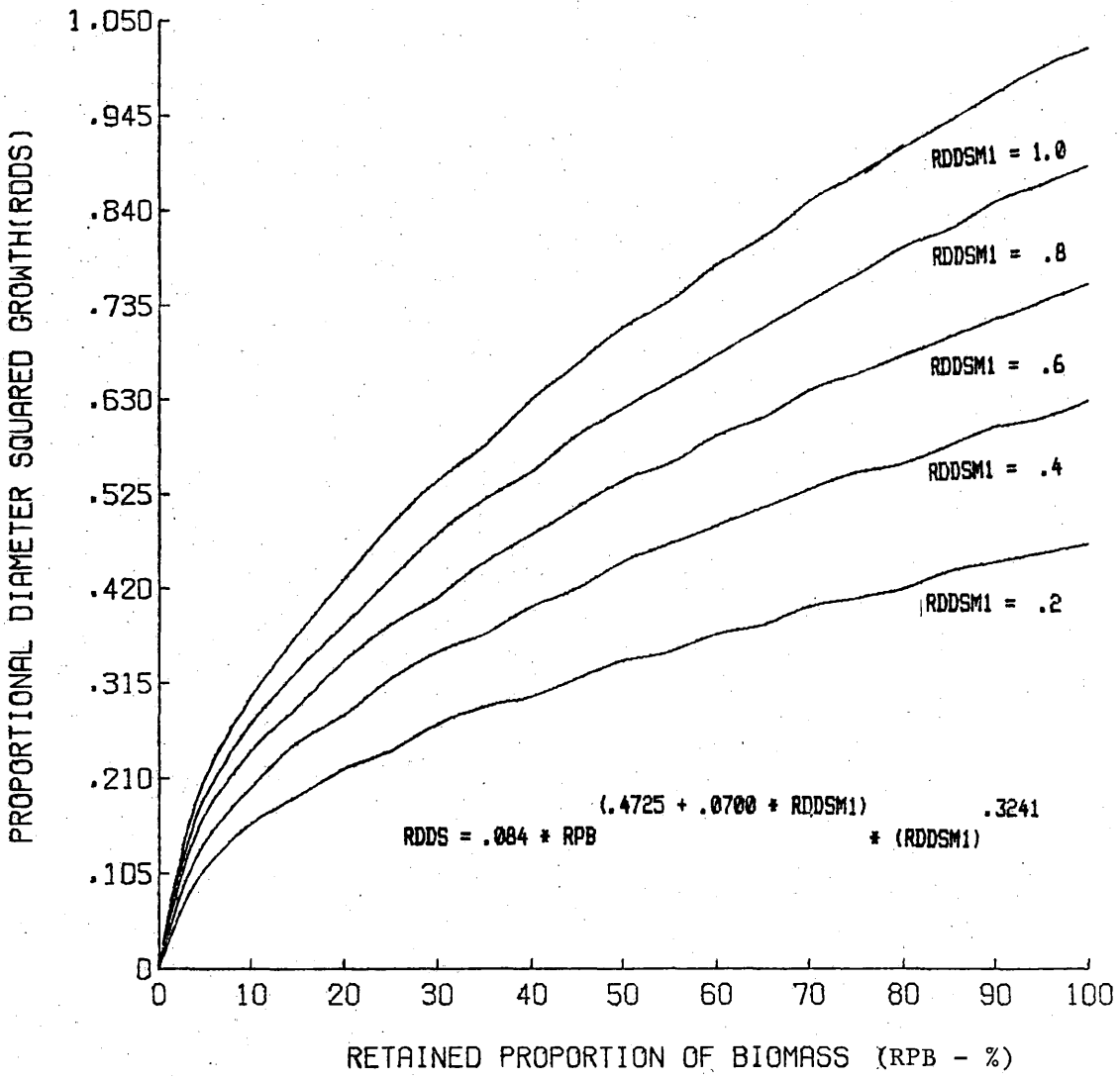

Figure 18. RDDS predicted from RPB and RDDSM1, using weather variables to adjust expected growth.

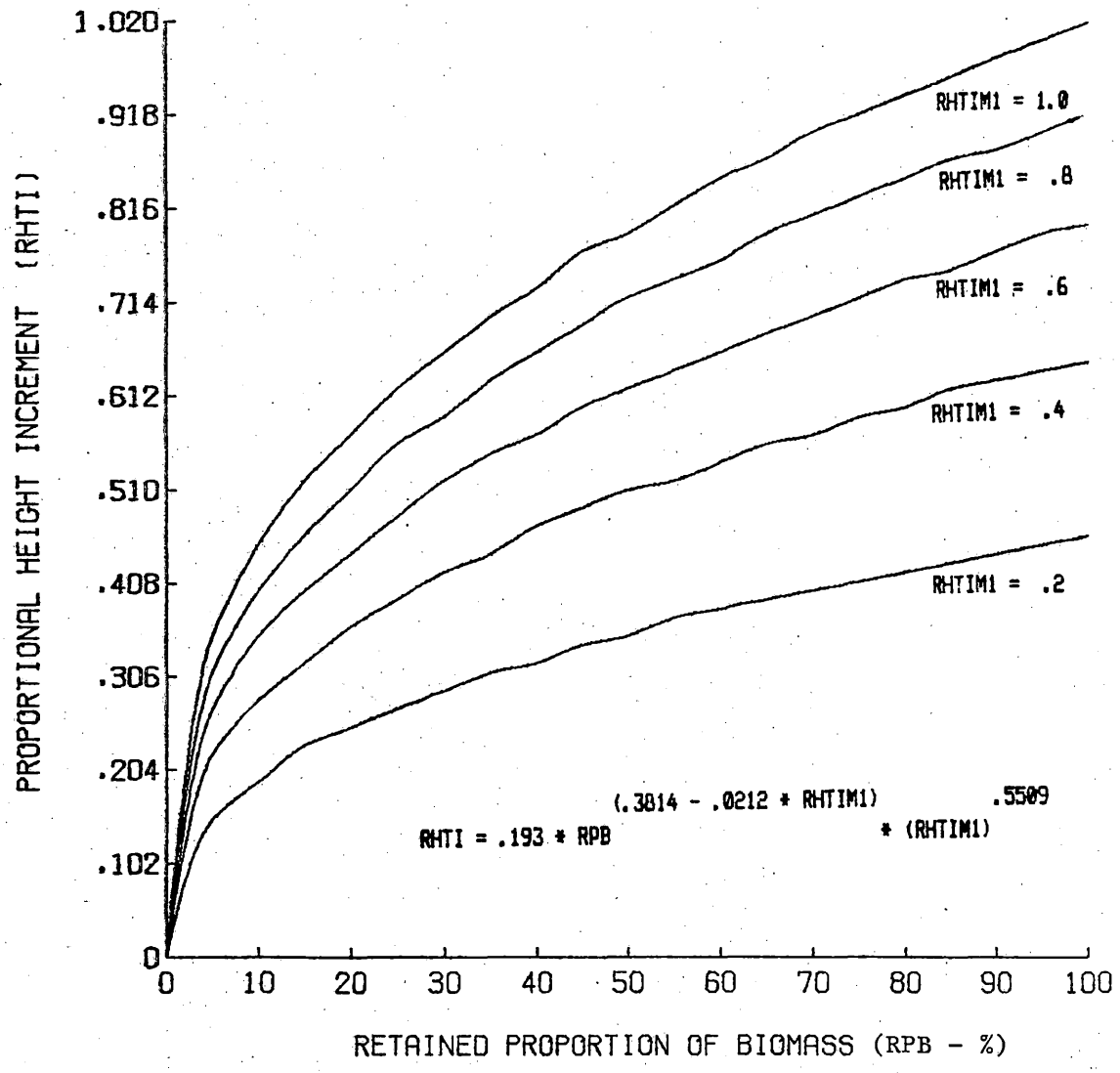

Figure 19. RHTI predicted from RPB and RDDSM1, using weather variables to adjust expected growth.

SUMMARY AND CONCLUSIONS

Relative basal area increment of nonhost trees and host trees was compared during periods of budworm activity and during periods without the effects of the budworm. Cumulative growth models were used in an attempt to provide estimates of the weather effects, but unexplained growth patterns of the nonhost trees precluded the use of these models. Instead, the ratios of annual growth to average growth for five year periods were used to describe differences between growing seasons.

These ratios were used to predict adjustments to annual host tree growth using nonhost tree growth, although the correlations were poor. Models predicting diameter growth from foliage and attack duration values yielded more logical results when these adjustments were used.

Weather variables (temperature, precipitation, and moisture stress) were also used to predict adjustments to annual growth. Diameter growth/foliage models computed using these adjustments yielded results very similar to those obtained when the nonhost tree growth correlations were used for the adjustments. Height growth/foliage models using these adjustments also yielded more logical results than those obtained without the adjustments.

Models using growth in the previous year as a measure of defoliation history for predicting diameter and height growth explained a larger amount of variation than models using attack

duration. These models should also be more representative of conditions on a greater number of areas. Use of this term in the models, however, could cause compounding of errors.

LITERATURE CITATIONS

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APPENDIX

Defoliation Variability

Data in the following tables represents summary statistics of defoliation data collected in 1982 under the research project "Growth Impacts on Host Trees Due to Western Spruce Budworm Defoliation on the Eastern Slope of the Washington Cascades". These statistics will be used by Dr. Kathy Sheehan of CANUSA to test insect/defoliation models she is developing.

Discussion of Methods

Data collection and sampling procedures for this project were given in detail in the May 1983 CANUSA report from the project noted above. The following is a general description of how this data was handled for obtaining the summary statistics, and describes the variables named in the tables.

The data was stratified into several categories : tree species (Douglas-fir and grand fir); height class (7-14 meters and over 14 meters); crown third (top, middle, and bottom); and defoliation class (0-15%, 15-40%, 40-65%, and 65+%). "Defoliation" was described using three separate descriptors: unadjusted current defoliation (ocular estimate of the proportion of foliage grazed on the current year's internode); adjusted current defoliation (proportion of current foliage grazed plus estimated loss of current foliage production caused by prior

defoliation - based on proportional branch internode length); and adjusted noncurrent defoliation (similar to adjusted current defoliation except computed from defoliation which occurred in the four preceding years).

The data set includes 7 years of estimates from each of 195 trees for the unadjusted current estimates, 7 years from 191 trees for the adjusted current defoliation estimates, and 3 years from 191 trees for the adjusted noncurrent estimates. Estimates per crown third were computed by averaging 2 sample branches (i.e., branches within a crown third were averaged before standard deviations were calculated).

Other estimates of variation are included in the tables. For each crown third of each tree each year, the differences between defoliation in the crown third and average defoliation in all crown thirds of the tree were calculated. In addition, the difference between defoliation of each crown third and average defoliation of all host trees in the stand was also calculated.

LIST OF VARIABLES IN TABLES

SUBSCRIPTS:

G = Stand
H = Tree
I = Crown third
J = Year

ARRAYS:

DEF = Unadjusted current defoliation - crown third.
TDEF = " " " - tree.
STDEF = " " " - stand.

ADEF = Adjusted current defoliation - crown third.
TADEF = " " " - tree.
STADEF = " " " - stand.

ADEFNC = Adjusted noncurrent defoliation - crown third.
TADEFNC = " " " - tree.
STADEFNC = " " " - stand.

Table A1. Unadjusted current defoliation - straight values (DEF(I,J)).

			HEIGHT=7-14m		HEIGHT)14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	2.0	0.0	2.6	2.3
		STD DEV	4.6	0.0	4.9	4.7
		NUMBER	77	6	518	136
	15 - 40%	MEAN	30.0	20.0	21.9	26.9
		STD DEV	22.4	0.0	17.8	16.5
		NUMBER	16	1	141	39
	40 - 65%	MEAN	38.1	35.0	46.0	49.9
		STD DEV	30.6	0.0	24.0	22.4
		NUMBER	16	1	103	37
	65+%	MEAN	84.9	94.6	86.3	88.1
		STD DEV	19.8	10.1	16.7	19.7
		NUMBER	24	6	169	75
MIDDLE	0 - 15%	MEAN	2.4	2.1	3.0	2.8
		STD DEV	4.8	2.5	5.5	6.4
		NUMBER	77	6	518	136
	15 - 40%	MEAN	16.9	22.5	22.6	20.7
		STD DEV	14.6	0.0	15.4	17.1
		NUMBER	16	1	141	39
	40 - 65%	MEAN	50.5	65.0	49.2	46.1
		STD DEV	21.2	0.0	19.4	19.8
		NUMBER	16	1	103	37
	65+%	MEAN	87.9	91.7	84.8	86.9
		STD DEV	16.1	15.8	15.2	14.7
		NUMBER	24	6	169	75
BOTTOM	0 - 15%	MEAN	4.0	3.8	3.6	2.8
		STD DEV	6.9	9.2	6.8	5.1
		NUMBER	77	6	518	136
	15 - 40%	MEAN	30.5	5.0	32.7	31.4
		STD DEV	19.4	0.0	21.0	17.8
		NUMBER	16	1	141	39
	40 - 65%	MEAN	63.8	45.0	58.4	56.1
		STD DEV	26.7	0.0	23.3	21.6
		NUMBER	16	1	103	37
	65+%	MEAN	83.0	84.2	82.8	85.0
		STD DEV	21.4	11.4	17.4	16.3
		NUMBER	24	6	169	75

Table A2. Unadjusted current defoliation - difference between crown third and tree average (DEF(I,J)-TDEF(H,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	-0.8	-1.9	-0.5	-0.3
		STD DEV	3.2	3.6	3.8	3.4
		NUMBER	77	6	518	136
	15 - 40%	MEAN	4.2	4.2	-3.8	0.5
		STD DEV	21.1	0.0	16.9	16.8
		NUMBER	16	1	141	39
	40 - 65%	MEAN	-12.7	-13.3	-5.2	-0.8
		STD DEV	27.0	0.0	21.9	22.2
		NUMBER	16	1	103	37
	65+%	MEAN	-0.4	4.4	1.7	1.5
		STD DEV	16.0	2.3	13.3	15.1
		NUMBER	24	6	169	75
MIDDLE	0 - 15%	MEAN	-0.4	0.1	-0.0	0.2
		STD DEV	3.7	2.5	3.8	4.6
		NUMBER	77	6	518	136
	15 - 40%	MEAN	-8.9	6.7	-3.2	-5.6
		STD DEV	14.6	0.0	14.1	14.1
		NUMBER	16	1	141	39
	40 - 65%	MEAN	-0.3	16.7	-2.0	-4.6
		STD DEV	21.4	0.0	18.0	16.6
		NUMBER	16	1	103	37
	65+%	MEAN	2.6	1.5	0.2	0.2
		STD DEV	13.2	7.0	10.4	11.0
		NUMBER	24	6	169	75
BOTTOM	0 - 15%	MEAN	1.2	1.8	0.5	0.2
		STD DEV	4.6	5.7	4.8	3.8
		NUMBER	77	6	518	136
	15 - 40%	MEAN	4.7	-10.8	7.0	5.1
		STD DEV	15.6	0.0	18.5	15.9
		NUMBER	16	1	141	39
	40 - 65%	MEAN	13.0	-3.3	7.2	5.4
		STD DEV	27.2	0.0	23.0	20.7
		NUMBER	16	1	103	37
	65+%	MEAN	-2.3	-6.0	-1.8	-1.7
		STD DEV	18.9	7.0	13.3	12.3
		NUMBER	24	6	169	75

Table A3. Unadjusted current defoliation - difference between crown third and stand average (DEF(I,J)-STDEF(G,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	STAND DEF					
TOP	0 - 15%	MEAN	-2.5	-1.5	-0.2	-0.8
		STD DEV	5.2	0.4	8.5	5.6
		NUMBER	73	6	506	136
	15 - 40%	MEAN	-3.8	12.3	-6.0	-2.5
		STD DEV	22.5	10.6	21.8	16.3
		NUMBER	19	2	143	25
	40 - 65%	MEAN	-0.9	35.3	0.6	-1.4
		STD DEV	28.7	12.4	29.2	25.6
		NUMBER	20	2	138	58
	65+%	MEAN	1.0	7.3	0.1	0.9
		STD DEV	21.8	4.5	24.1	20.0
		NUMBER	21	4	144	68
MIDDLE	0 - 15%	MEAN	-1.9	0.6	-0.1	0.3
		STD DEV	5.0	2.4	8.2	10.3
		NUMBER	73	6	506	136
	15 - 40%	MEAN	4.8	28.5	-3.1	3.5
		STD DEV	23.7	30.1	20.7	27.5
		NUMBER	19	2	143	25
	40 - 65%	MEAN	-1.6	31.6	0.9	-12.9
		STD DEV	34.1	28.3	27.3	23.2
		NUMBER	20	2	138	58
	65+%	MEAN	-3.7	4.8	-0.7	0.3
		STD DEV	25.9	7.7	21.0	15.7
		NUMBER	21	4	144	68
BOTTOM	0 - 15%	MEAN	-0.3	2.2	1.0	0.3
		STD DEV	6.3	9.0	10.0	7.5
		NUMBER	73	6	506	136
	15 - 40%	MEAN	12.2	9.8	4.5	11.1
		STD DEV	29.8	28.3	25.8	22.1
		NUMBER	19	2	143	25
	40 - 65%	MEAN	1.4	24.1	5.3	-4.6
		STD DEV	31.8	3.5	26.4	25.4
		NUMBER	20	2	138	58
	65+%	MEAN	1.9	-2.7	-0.1	0.1
		STD DEV	21.3	9.8	20.4	14.0
		NUMBER	21	4	144	68

Table A4. Adjusted current defoliation - straight values (ADEF(I,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	0.7	11.7	-0.1	2.2
		STD DEV	9.3	10.2	8.5	9.2
		NUMBER	42	7	197	50
	15 - 40%	MEAN	19.0	33.3	19.8	27.0
		STD DEV	23.0	11.1	20.8	18.3
		NUMBER	66	6	232	61
	40 - 65%	MEAN	44.0	51.0	47.9	48.3
		STD DEV	22.6	8.9	18.8	17.4
		NUMBER	54	3	160	60
	65+%	MEAN	88.0	95.6	84.3	83.7
		STD DEV	15.8	6.5	16.7	19.4
		NUMBER	69	12	223	95
MIDDLE	0 - 15%	MEAN	3.7	-1.3	2.0	3.7
		STD DEV	9.5	4.7	8.7	8.6
		NUMBER	42	7	197	50
	15 - 40%	MEAN	23.9	15.0	21.6	23.2
		STD DEV	15.5	12.3	16.4	17.4
		NUMBER	66	6	232	61
	40 - 65%	MEAN	45.9	37.0	50.3	46.2
		STD DEV	17.5	8.5	17.3	17.9
		NUMBER	54	3	160	60
	65+%	MEAN	85.5	81.2	85.2	86.4
		STD DEV	15.2	20.1	14.9	13.7
		NUMBER	69	12	223	95
BOTTOM	0 - 15%	MEAN	15.9	8.3	12.4	6.7
		STD DEV	13.3	11.1	14.8	12.2
		NUMBER	42	7	197	50
	15 - 40%	MEAN	39.0	18.8	37.9	37.4
		STD DEV	17.7	17.4	20.1	18.8
		NUMBER	66	6	232	61
	40 - 65%	MEAN	65.5	67.0	55.1	56.6
		STD DEV	18.1	27.1	18.7	19.8
		NUMBER	54	3	160	60
	65+%	MEAN	86.9	84.4	87.1	86.8
		STD DEV	14.4	12.3	13.1	12.7
		NUMBER	69	12	223	95

Table A5. Adjusted current defoliation - difference between crown third and tree average (ADEF(I,J)-TADEF(H,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	-6.1	5.5	-4.9	-2.0
		STD DEV	9.7	5.0	8.1	7.6
		NUMBER	42	7	197	50
	15 - 40%	MEAN	-8.3	10.9	-6.7	-2.2
		STD DEV	20.0	11.7	18.6	18.1
		NUMBER	66	6	232	61
	40 - 65%	MEAN	-7.8	-0.7	-3.2	-2.1
		STD DEV	21.2	9.8	18.3	17.1
		NUMBER	54	3	160	60
	65+%	MEAN	1.2	8.5	-1.2	-1.9
		STD DEV	10.8	6.5	11.3	12.3
		NUMBER	69	12	223	95
MIDDLE	0 - 15%	MEAN	-3.1	-7.5	-2.7	-0.5
		STD DEV	7.6	7.9	8.3	7.4
		NUMBER	42	7	197	50
	15 - 40%	MEAN	-3.4	-7.4	-4.8	-6.0
		STD DEV	13.4	12.7	13.7	15.7
		NUMBER	66	6	232	61
	40 - 65%	MEAN	-5.9	-14.7	-0.8	-4.2
		STD DEV	16.8	12.8	14.7	15.8
		NUMBER	54	3	160	60
	65+%	MEAN	-1.3	-5.9	-0.4	0.8
		STD DEV	9.1	10.5	9.4	8.7
		NUMBER	69	12	223	95
BOTTOM	0 - 15%	MEAN	9.2	2.0	7.6	2.6
		STD DEV	11.0	7.0	11.4	8.2
		NUMBER	42	7	197	50
	15 - 40%	MEAN	11.7	-3.6	11.5	8.2
		STD DEV	19.1	11.3	20.5	16.4
		NUMBER	66	6	232	61
	40 - 65%	MEAN	13.7	15.3	4.0	6.3
		STD DEV	16.9	22.2	17.2	17.6
		NUMBER	54	3	160	60
	65+%	MEAN	0.1	-2.6	1.6	1.2
		STD DEV	11.6	7.8	10.8	10.1
		NUMBER	69	12	223	95

Table A6. Adjusted current defoliation - difference between crown third and stand average (ADEF(I,J)-STADEF(G,J)).

			HEIGHT=7-14m		HEIGHT)14m	
			DF	GF	DF	GF
	STAND DEF					
TOP	0 - 15%	MEAN	-5.9	0.0	-6.2	-2.8
		STD DEV	14.2	0.0	12.2	18.7
		NUMBER	26	0	148	28
	15 - 40%	MEAN	-6.8	-4.1	-6.6	-3.7
		STD DEV	20.8	14.7	23.2	19.5
		NUMBER	104	13	301	91
	40 - 65%	MEAN	5.5	10.3	-5.4	-0.8
		STD DEV	28.6	20.7	27.9	21.3
		NUMBER	45	6	147	55
	65+%	MEAN	5.1	11.5	-1.3	-1.1
		STD DEV	12.8	10.9	19.2	21.1
		NUMBER	56	9	216	92
MIDDLE	0 - 15%	MEAN	2.5	0.0	-1.7	0.3
		STD DEV	18.5	0.0	13.2	23.1
		NUMBER	26	0	148	28
	15 - 40%	MEAN	0.4	-19.2	-5.4	-0.4
		STD DEV	21.1	13.5	21.6	21.5
		NUMBER	104	13	301	91
	40 - 65%	MEAN	1.6	-10.5	-3.8	-4.5
		STD DEV	26.7	15.2	24.9	28.3
		NUMBER	45	6	147	55
	65+%	MEAN	-2.4	0.9	-0.7	-3.4
		STD DEV	20.9	10.0	19.4	21.0
		NUMBER	56	9	216	92
BOTTOM	0 - 15%	MEAN	13.4	0.0	6.7	-0.5
		STD DEV	17.3	0.0	17.1	19.8
		NUMBER	26	0	148	28
	15 - 40%	MEAN	15.9	-14.3	8.9	8.6
		STD DEV	23.2	11.3	22.8	21.5
		NUMBER	104	13	301	91
	40 - 65%	MEAN	11.3	15.3	2.7	6.1
		STD DEV	24.0	11.5	23.6	25.6
		NUMBER	45	6	147	55
	65+%	MEAN	3.6	1.0	1.8	-0.1
		STD DEV	14.6	14.4	16.5	16.2
		NUMBER	56	9	216	92

Table A7. Adjusted noncurrent defoliation - straight values (ADEFNC(I,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	20.0	0.0	9.2	16.4
		STD DEV	5.4	0.0	8.7	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	27.4	0.0	25.5	39.1
		STD DEV	17.7	0.0	13.2	10.6
		NUMBER	14	0	63	16
	40 - 65%	MEAN	51.0	67.0	51.1	52.4
		STD DEV	13.8	7.7	13.4	12.6
		NUMBER	50	7	139	39
	65+%	MEAN	78.2	85.7	72.2	72.1
		STD DEV	12.6	9.9	11.5	11.6
		NUMBER	32	5	137	58
MIDDLE	0 - 15%	MEAN	-2.8	0.0	6.1	17.3
		STD DEV	0.2	0.0	5.1	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	32.2	0.0	26.8	31.6
		STD DEV	10.1	0.0	10.0	10.3
		NUMBER	14	0	63	16
	40 - 65%	MEAN	46.4	45.0	51.2	52.1
		STD DEV	12.8	11.9	10.5	14.4
		NUMBER	50	7	139	39
	65+%	MEAN	74.1	66.2	75.4	74.8
		STD DEV	13.2	6.0	9.4	10.2
		NUMBER	32	5	137	58
BOTTOM	0 - 15%	MEAN	7.9	0.0	19.6	7.3
		STD DEV	1.7	0.0	9.1	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	35.9	0.0	37.6	26.2
		STD DEV	10.9	0.0	13.1	10.7
		NUMBER	14	0	63	16
	40 - 65%	MEAN	64.9	59.6	58.7	60.8
		STD DEV	12.6	10.2	14.2	10.5
		NUMBER	50	7	139	39
	65+%	MEAN	79.8	76.7	78.4	80.7
		STD DEV	10.2	9.7	8.9	8.8
		NUMBER	32	5	137	58

Table A8. Adjusted noncurrent defoliation - difference between crown third and tree average (ADEFNC(I,J)-TADEFNC(H,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	TREE DEF					
TOP	0 - 15%	MEAN	11.6	0.0	-2.4	2.8
		STD DEV	3.0	0.0	7.7	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	-4.4	0.0	-4.5	6.8
		STD DEV	15.5	0.0	10.3	7.5
		NUMBER	14	0	63	16
	40 - 65%	MEAN	-3.1	9.8	-2.5	-2.7
		STD DEV	9.6	5.5	11.2	12.8
		NUMBER	50	7	139	39
	65+%	MEAN	0.8	9.5	-3.1	-3.8
		STD DEV	8.8	4.7	8.3	7.9
		NUMBER	32	5	137	58
MIDDLE	0 - 15%	MEAN	-11.2	0.0	-5.5	3.6
		STD DEV	2.1	0.0	4.5	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	0.4	0.0	-3.2	-0.7
		STD DEV	11.7	0.0	8.0	8.0
		NUMBER	14	0	63	16
	40 - 65%	MEAN	-7.7	-12.2	-2.5	-3.0
		STD DEV	11.1	7.5	8.3	11.8
		NUMBER	50	7	139	39
	65+%	MEAN	-3.3	-10.0	0.1	-1.1
		STD DEV	7.8	5.8	5.9	6.6
		NUMBER	32	5	137	58
BOTTOM	0 - 15%	MEAN	-0.5	0.0	8.0	-6.4
		STD DEV	1.1	0.0	9.9	0.0
		NUMBER	3	0	9	1
	15 - 40%	MEAN	4.0	0.0	7.6	-6.1
		STD DEV	8.3	0.0	10.8	7.3
		NUMBER	14	0	63	16
	40 - 65%	MEAN	10.8	2.4	5.0	5.7
		STD DEV	11.9	10.7	12.1	6.9
		NUMBER	50	7	139	39
	65+%	MEAN	2.5	0.5	3.0	4.9
		STD DEV	8.9	7.7	6.9	6.1
		NUMBER	32	5	137	58

Table A9. Adjusted noncurrent defoliation - difference between crown third and stand average (ADEFNC(I,J)-STADEFNC(G,J)).

			HEIGHT=7-14m		HEIGHT>14m	
			DF	GF	DF	GF
	STAND DEF					
TOP	0 - 15%	MEAN	0.0	0.0	0.0	0.0
		STD DEV	0.0	0.0	0.0	0.0
		NUMBER	0	0	0	0
	15 - 40%	MEAN	-6.4	0.0	-1.9	-3.5
		STD DEV	10.5	0.0	17.7	10.0
		NUMBER	14	0	59	8
	40 - 65%	MEAN	0.8	10.7	-3.4	-0.2
		STD DEV	14.5	8.3	16.8	13.1
		NUMBER	60	5	142	42
	65+%	MEAN	6.6	11.8	-4.5	-4.9
		STD DEV	14.7	10.9	14.8	15.3
		NUMBER	25	7	147	64
MIDDLE	0 - 15%	MEAN	0.0	0.0	0.0	0.0
		STD DEV	0.0	0.0	0.0	0.0
		NUMBER	0	0	0	0
	15 - 40%	MEAN	-1.2	0.0	0.8	-3.3
		STD DEV	17.1	0.0	14.9	11.1
		NUMBER	14	0	59	8
	40 - 65%	MEAN	-3.1	-14.2	-4.0	-7.0
		STD DEV	18.2	8.0	15.2	14.7
		NUMBER	60	5	142	42
	65+%	MEAN	-1.3	-6.4	-1.6	0.0
		STD DEV	16.8	7.8	14.6	14.9
		NUMBER	25	7	147	64
BOTTOM	0 - 15%	MEAN	0.0	0.0	0.0	0.0
		STD DEV	0.0	0.0	0.0	0.0
		NUMBER	0	0	0	0
	15 - 40%	MEAN	5.8	0.0	4.1	-11.8
		STD DEV	19.6	0.0	13.4	13.6
		NUMBER	14	0	59	8
	40 - 65%	MEAN	12.3	2.2	5.4	-0.1
		STD DEV	17.2	8.1	14.0	17.0
		NUMBER	60	5	142	42
	65+%	MEAN	5.4	4.1	3.3	5.8
		STD DEV	9.7	10.9	12.7	12.7
		NUMBER	25	7	147	64